POST-FIRE VARIABILITY IN SIBERIAN ALDER IN INTERIOR ALASKA: DISTRIBUTION PATTERNS, NITROGEN FIXATION RATES, AND ECOSYSTEM CONSEQUENCES

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ABSTRACT

The circumpolar boreal forest is responsible for a considerable proportion of global carbon sequestration and is an ecosystem with limited nitrogen (N) pools. Boreal forest fires are predicted to increase in severity, size, and frequency resulting in increased losses of N from this system due to volatilization. Siberian alder (*Alnus viridis ssp. fruticosa*) N-fixation is a significant source of N-input within the interior Alaskan boreal forest and likely plays a pivotal, though poorly understood, role in offsetting losses of N due to fire. This study disentangles the effects of fire severity, post-fire age, and environmental variables on Siberian alder N-input across the upland boreal forest and quantifies the landscape-level implications of Siberian alder N-input on N pool balance. Stand types of an early- and intermediate-age burn scar were determined by relevé plot sampling, hierarchical clustering, and indicator species analysis. Alder growth traits (density, nodule biomass, nodule N-fixation, and other traits) were sampled across all stand types, burn scars, and a fire severity gradient. Pre- and post-fire landscape-level N-fixation inputs were quantified within the early-age burn scar by scaling-up Siberian alder growth traits to the stand-level and then mapping the total area of pre- and post-fire stand types.

Results show that fire severity shares a complex relationship with Siberian alder N-input in black spruce stands, wherein moderate fire severity has a negligible effect on Siberian alder N-input, moderate to high fire severity increases Siberian alder N-input, and high fire severity reduces Siberian alder N-input. Fire likely limited alder vegetative propagation in post-fire black spruce trajectory stands but enhanced propagation in post-fire deciduous trajectory stands that experienced moderate severity. Following the 2004 Boundary Fire, Siberian alder N-input showed an overall increase across the landscape, mostly within post-fire deciduous stand types.

Future increases of fire severity and subsequent conversions of stand type from black spruce to deciduous dominance have the potential to increase total short-term N-input on the landscape, but a majority of those gains will be concentrated within a small proportion of the post-fire landscape (i.e. deciduous trajectory stand types). In the boreal forest, the temporal and spatial pattern of ecosystem processes that rely on N fixation inputs is dependent on the recruitment and growth of Siberian alder, which is in turn dependent on a complex relationship between fire severity, stand type, and post-fire age.

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INTRODUCTION

The boreal forest covers 11% of Earth's terrestrial surface and comprises nearly one-third of all forested land globally (Bonan and Shugart 1989, Bonan 2008). Additionally, boreal forests contain 16% of total forest carbon (C) stocks (~ 250 Pg C), and are responsible for nearly 13% of the C that is sequestered by forests each year (0.5 Pg C yr^{-1}) (Bonan 2008, Pan et al. 2011). The availability of soil nitrogen (N) constrains the sequestration of C in response to elevated CO_2 (Reich et al. 2006), especially in N-limited systems such as the boreal forest (Tamm 1990, Högberg et al. 2017). Available N may become more limiting as N accumulates in litter and plant biomass under elevated levels of atmospheric CO_2 (Hungate et al. 2004, van Groenigen et al. 2006), which would further exacerbate the need for additional N to sequester continually increasing atmospheric CO_2 (Fischlin et al. 2007). Future levels of C sequestration in the boreal forest will depend on the difference between losses of N through such processes as volatilization during wildfire (Brais et al. 2000, Wirth et al. 2002, Boby et al. 2010), and N-gains due to biological N-fixation (Lüscher et al. 2000, DeLuca et al. 2002, Palviainen et al. 2017) and the atmospheric deposition of N (Berendse et al. 2001, Matson et al. 2002). Because most of the boreal forest receives atmospheric N-deposition at rates lower than biological N-fixation (Dentener et al. 2006, Gundale et al. 2011), N supplies from sources such as bryophyte N-fixation (Deluca et al. 2002, Zackrisson et al. 2009, Palviainen et al. 2017) and alder N-fixation (Van Cleve et al. 1971, Anderson et al. 2004, Ruess et al. 2013) have the largest impact on N balance in the boreal forest. Boreal forest alder N-input (up to 140 kg N ha^{-1} yr^{-1}) (Anderson et al. 2004, Mitchell and Ruess 2009, Ruess et al. 2009, Ruess et al. 2013) can be substantially higher than N-fixation by

bryophytes (0.1 to 4 kg N ha^{-1} yr^{-1}) (Deluca et al. 2002, Zackrisson et al. 2009), though the distribution (total area) of alder cover in the boreal forest is poorly understood. Accurate estimates of alder N-fixation inputs are a key component of ecosystem N balance equations in the boreal forest, and therefore integral toward predicting N limitations on global C sequestration.

Within the Alaskan boreal forest, thin-leaf alder (*Alnus incana ssp. tenufolia*) N-fixation contributions range from about 19 to 140 kg N ha^{-1} yr^{-1} (Van Cleve et al. 1971, Uliassi and Ruess 2002, Anderson et al. 2004, Ruess et al. 2009, Ruess et al. 2013), which accounts for nearly all of the N accumulated in a 150-year-old floodplain forest (Uliassi and Ruess 2002). Though patch-scale inputs by *A. incana* can be high, the shrub is restricted typically to early successional river bars, particularly where abundant herbivory by moose on willows indirectly aids alder growth and dominance (Butler and Kielland 2008, Nossov et al. 2011). Siberian alder (*Alnus viridis ssp. fruticosa;* hereafter, *A. fruticosa*), which has been estimated to fix between 2 and 10 kg N ha^{-1} yr^{-1} (Anderson et al. 2004, Mitchell and Ruess 2009), is the more spatially dominant *Alnus* species in the northern boreal forests of Alaska and is distributed primarily (but not exclusively) throughout mesic to subxeric soils of upland forests that cover a greater area than floodplain forests. Siberian alder is also more abundant than thin-leaf alder across poorly drained soils and water tracks in upland regions, and is the predominant alder species throughout the northern boreal forest within Alaska and western Canada. However, within-stand distribution patterns of *A. viridis* are difficult to describe because individual shrubs are spatially aggregated by genet, which complicates spatial predictions of *A. viridis* N-inputs. Several studies of alder in the interior Alaskan boreal forest have quantified alder N-fixation (kg N ha^{-1} yr^{-1}) at the patch-scale (e.g. study plots),

but they haven't included a spatially large distribution of study plots across vegetation types that can address the within-stand density variation of alder patches that can be scaled to the landscape (Van Cleve et al. 1971, Uliassi and Ruess 2002, Anderson et al. 2004, Mitchell and Ruess 2009, Ruess et al. 2013). Where Siberian alder density is high, N-fixation inputs are also high. As such, the density of alder within and among different stand types, and the landscape area covered by each stand type, will determine whether Siberian alder N-fixation inputs constitute a major source of N-input at the landscape-scale of the Alaskan boreal forests.

Aside from its potential as a regionally important N-fixer, Siberian alder's N-inputs also play a role in several stand, community and landscape-level ecosystem processes such as N pool accretion, woody plant competition, soil acidification, and aquatic productivity. As a long-lived perennial shrub, alder genets continually propagate throughout succession by vegetative reproduction from the root crown and rhizomes. Patches of alder often colonize bare, nutrient-poor, mineral soil by seed (Zasada et al. 1983, Chapin et al. 1994, Lantz et al. 2010) where N-rich leaf litter and nodule and root turnover by alder significantly boosts N pools. Positive feedbacks of alder N-input include boosted aquatic productivity in streams and lakes during primary and secondary succession (Crocker and Major 1955, Hu et al. 2001, Shaftel et al. 2012) and high forest growth and productivity (C storage) especially during early succession (Heilman et al. 1966, Van Cleve et al. 1971, Wurtz 1995, Uliassi and Ruess 2002, Mitchell and Ruess 2009). Yet negative feedbacks of alder also exist, such as the shrub's largely inhibitory effects (e.g. shading and competition) on tree growth in early to middle-age succession white spruce stands (Chapin et al. 2016, Cortini and Comeau 2008), and the lowering of soil pH beneath and adjacent to alder canopies (Franklin et al. 1968, Hu

et al. 2001, Mitchel and Ruess 2009), which can lead to a decline in soil fertility or nutrient imbalances beneath and adjacent to legacy patches of alder (van Miegroet and Cole 1984). Siberian alder's ecological impact is not limited to N-fixation inputs, and effects are largely stand and site-characteristic dependent (Chapin et al. 2016). However, Siberian alder's abundant colonization and reproduction throughout succession, combined with persistent nodule growth (Mitchell and Ruess et al. 2009, Anderson et al. 2004) and N-fixation capacity (Mitchell and Ruess 2009), can lead to high N-inputs in late-stage secondary succession (Mitchell and Ruess 2009) that contribute significantly to N pool balance in the boreal forest.

Across the Alaskan boreal forest, fire severity and extent are both increasing while fire return intervals are decreasing (Kasischke et al. 2010, Calef et al. 2015). Increased severity of the fire regime increases boreal forest vulnerability to C and N loss (Kasischke et al. 2011, Boby et al. 2010, Palviainen et al. 2017) as well as the destruction of N-fixers such as bryophytes and alder (DeLuca et al. 2008, Mitchell and Ruess 2009, Palviainen et al. 2017), potentially disrupting ecosystem processes and C and N pool balance across several spatial scales. Direct impacts of fire on Siberian alder N-input at the landscape- and regional-level are poorly understood, primarily because Siberian alder distribution has not been accurately mapped regionally, and N-fixation has not been quantified across fire severity gradients within multiple stand types of the Alaskan boreal forest. Yet, Siberian alder is often one of the earliest colonizers of burned boreal forest (Haeussler et al. 1990), especially where newly exposed mineral seedbeds are a productive medium for alder (Lantz et al. 2010, Zasada et al. 1983). Pre-fire Siberian alder meristems that are not burned by fire have been known to regenerate (Rowe and Scotter 1973, Gilbert and Payette 1982), though severe fire that burns deep into organic soil horizons can kill alder rhizomes and reduce post-fire sprouting (Zasada

1986). Where alder is present before fire, it is heavily favored in post-fire colonization and regrowth compared to surrounding non-N-fixing plants (Healy and Gill 1974). Taken together, previous studies suggest that low- to moderate-severity fire will facilitate Siberian alder growth and expansion, especially in pre-fire alder stands and adjacent areas of newly exposed mineral soil. Furthermore, the persistent regrowth of alder populations post-fire (Mitchell and Ruess 2009, Rowe 1983) would suggest that successive fire cycles of low to moderate fire severity have likely favored increased Siberian distribution and associated N-input across the boreal forest for centuries, and potentially millennia. Given that high fire severity can reduce alder populations (Zasada (1986), a future fire regime dominated by high severity fire and shorter return-intervals may result in decreasing alder N-input – at least initially. Evidence already suggests that net-losses of N due to combustion have occurred in the boreal forest over the past 6500 years (Harden et al. 2002), but the amount of N-loss offset by post-fire N-fixation is unknown. An increasingly severe fire regime may increase the rate of N-loss while decreasing the rate of N-recovery by N-fixers such as Siberian alder.

Siberian alder is one of the most important N-fixers in the circumpolar boreal forest. If Siberian alder's spatial distribution within stand types and across ecoregions is not severely limited by high fire severity (i.e. the destruction of alder populations), high rates of plant-level alder N-input may have the potential to offset N losses from the increasingly severe fire regime that is predicted in the boreal forest. The primary goal of this thesis is the spatially explicit examination of Siberian alder density, growth, and N-fixation across a fire severity and fire age gradient within stand types of both an 11-year-old and a 44-year-old burn scar of the interior Alaskan boreal forest. I have divided this thesis into two chapters. Chapter 1 outlines the patterns as well as the biotic (topoedaphic variables) and abiotic (fire severity

and post-fire age) controls of alder growth traits (density, growth, and N-fixation) at the plot and stand level, with a special emphasis on stand-level N-fixation input (kg N ha stand type^{-1} yr^{-1}). Chapter 2 focuses on the relationship between fire severity, fire age, and stand-level N-fixation input, and the implications of that relationship and post-fire stand type distribution on the spatial patterns of landscape-level N balances.

CHAPTER 1: CAN SIBERIAN ALDER N-FIXATION OFFSET N-LOSS AFTER SEVERE FIRE IN BOREAL ALASKA? QUANTIFYING POST-FIRE ALDER DISTRIBUTION, GROWTH, AND NITROGEN-FIXATION IN TWO BURN SCARS IN THE YUKON-TANANA ECOREGION[1]

Abstract

Siberian alder (*Alnus viridis ssp. fruticosa*) forms a symbiotic relationship with the nitrogen-fixing *Frankia* bacteria in Alaskan ecosystems and is therefore a significant contributor of nitrogen (N) in post-disturbance ecosystems. The effect of fire severity on Siberian alder annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}) across black spruce (*Picea mariana* (Mill.) BSP) forests of interior Alaska is largely unknown. We hypothesized that increasing fire severity in the boreal forest directly reduces Siberian alder populations and therefore annual stand-level N-fixation inputs. Our specific objectives were to quantify annual stand-level N-fixation input between an early-age and intermediate-age burn scar, across a fire severity gradient, and among vegetation types. Annual stand-level N-fixation input was comparable between the early-age and intermediate-age burn scars (2.75 ± 0.08 and 2.91 ± 0.06 kg N ha^{-1} yr^{-1}, respectively). Siberian alder fixed 0.06 ± 0.003 kg N ha^{-1} yr^{-1} in high severity black spruce stands of the early-age burn scar, which was 88% and 97% lower than Siberian alder stand-level N-fixation N-inputs for moderate, and moderate-to-high severity black spruce stands. Annual stand-level N-fixation inputs in the black spruce vegetation type were 82% and 92% lower than in the deciduous vegetation type for intermediate-age and early-age burn scars, respectively. The

[1] Houseman, B.R., Hollingsworth, T.N., Ruess, R.W., & Verbyla, D.L. (in preparation). Can Siberian Alder N-fixation offset N-loss after severe fire in boreal Alaska? Quantifying post-fire alder distribution, growth, and nitrogen fixation in two burn scars in the Yukon-Tanana Uplands. *Global Change Biology*.

results of this study outline a possible threshold in the fire-alder relationship beyond which extreme fire severity can effectively lower Siberian alder N-inputs. When combined with stand conversions from black spruce to deciduous after fire, Siberian alder N-inputs are unlikely to offset losses N due to fire or supply enough N for deciduous stand growth during post-fire secondary succession.

INTRODUCTION

Siberian alder (*Alnus viridis ssp. fruticosa*) forms a symbiotic relationship with the nitrogen-fixing *Frankia* bacteria in Alaskan ecosystems. Because of this symbiotic relationship, the presence of alder (*Alnus ssp.*) in post-disturbance ecosystems could have significant implications for nitrogen (N) inputs (up to 59 kg $N \cdot ha^{-1} \cdot yr^{-1}$) (Van Cleve et al. 1971, Van Cleve et al. 1983a, Van Cleve et al. 1993, Uliassi and Ruess 2002). Alder symbiotic N-fixation is associated with substantial increases to ecosystem N pools in early succession along floodplains (Van Cleve et al. 1991, Uliassi and Ruess 2002, Nossov et al. 2011), in terrestrial and aquatic systems following glacial retreat (Crocker and Major 1955, Fastie 1995, Engstrom et al. 2000), and in post-fire secondary succession of boreal forest uplands (Van Cleve et al. 1983a, Uliassi and Ruess 2002, Mitchell and Ruess 2009a). These studies, conducted at limited spatial scales, show a linkage between alder stands and high rates of N-fixation inputs and nutrient cycling during primary and secondary succession. No studies have estimated annual stand-level N-fixation input across a gradient of fire severity in the pre-fire black spruce (*Picea mariana* (Mill.) BSP) forests that comprise a majority of interior Alaska, therefore the effect of fire severity on Siberian alder N-input across the landscape of interior Alaska is largely unknown.

Alder distribution and associated N-fixation inputs can affect regional biogeochemical patterns. Hu et al. (2001) suggested that during the mid-Holocene, alder expansion was associated with increased N cycling and availability, elevated aquatic productivity, and soil acidification in western Alaska. Watershed biogeochemical patterns are also strongly influenced by the presence and abundance of alder. In Oregon, alder-dominated stands increase regional stream N exports (Compton et al. 2003), and on the Kenai Peninsula, Alaska, variations in alder cover strongly impact nitrate concentrations of headwater streams, that in turn influence primary production in juvenile salmonid habitat (Shaftel et al. 2012). However, the drivers and consequences of alder distribution and abundance in a post-fire landscape remain unclear.

Climate warming in interior Alaska over the past 60 years (Bieniek et al. 2014) has resulted in wildfires becoming more frequent and severe across the boreal forest (Calef et al. 2015). With a shift in fire regime, there may be an associated shift in dominant vegetation from black spruce to deciduous forest in areas of high fire severity (Johnstone et al. 2010). Wildfire combustion of soil organic matter (where most N is held) varies considerably with fire severity and forest-floor moisture content (Kasischke et al. 1995). On average, approximately 50% of soil organic N in burned black spruce stands was combusted during the 2004 Alaska fire season (Boby et al. 2010). Despite the importance of fire in shaping community and ecosystem dynamics in the boreal forest (Hollingsworth et al. 2013), little is known about the effect of fire on alder density, growth, and N-fixation (collectively referred to as alder growth traits) and the subsequent effects on ecosystem dynamics throughout secondary succession. Lantz et al. (2010) found that fire could facilitate alder expansion in the boreal forest via increased alder growth and reproduction on burned sites. Schimmel and Granstrom (1996) found that depth of burn was positively correlated with reduced shrub density for those shrubs that reproduce from rhizomes

(such as alder). Yet, successful alder recruitment is dependent on the current spatial distribution of alder, as well as the patterns and controls over alder growth and N-fixation across various upland vegetation types (e.g. black spruce- versus deciduous-dominant) both of which are not known. Therefore, annual stand-level Siberian alder N-fixation inputs are difficult to estimate.

The Bonanza Creek Long-Term Ecological Research (BNZ LTER) program has studied vegetation structure and ecosystem function in replicated stands following the 1983 Rosie Creek fire that burned 2,771 ha of mature white spruce forest (Chapin et al. 2010). Whereas successional models derived from those studies emphasize the prominent role of Siberian alder in ecosystem development (Van Cleve et al. 1991, Hollingsworth et al. 2010, Mitchell and Ruess 2009a), other more regionally extensive studies of black spruce forests indicate that Siberian alder distribution does not appear dense nor continuous across the region (Hollingsworth 2004, Hollingsworth et al. 2013). One of the primary difficulties in scaling plant N-input has been uncertainty in the spatial distribution of the putative N-fixing plants (Herridge et al. 2008). Accurately scaling alder N-inputs within the black spruce forests will require addressing the spatial distribution of alder.

Understanding the effect of Alaska's changing fire regime on alder growth traits and alder's effect on post-fire N balance requires extensive study of the patterns and controls over alder N inputs and their relationship to fire effects at a landscape scale. To assess the current impact of alder on terrestrial ecosystem function at larger landscape and regional scales, alder growth traits should be sampled across complex landscapes with different vegetation types and disturbance histories. We hypothesized that increasing fire severity in the boreal forest directly reduces Siberian alder populations and therefore annual stand-level N-fixation inputs. Our specific objectives were to 1) quantify the variation of alder growth traits (alder density, growth,

and N-fixation) between an early-age and intermediate-age burn scar, across a fire severity gradient in an early-age fire, and among vegetation types, and 2) model alder growth traits by environmental characteristics and fire severity at patch and landscape scales.

METHODS

Study Area

The study area encompassed two burn scars in the Yukon-Tanana Uplands ecoregion (Nowacki et al. 2001) north of Fairbanks, Alaska (Figure 1.1). The Wickersham Dome Fire, which burned 5,500 ha in 1971, is located approximately 35 km NW of Fairbanks, Alaska (64.9° N, 147.9° W) and was considered moderate to low severity. The Boundary Fire burned over 210,000 ha in 2004 and is located approximately 40 km NE of Fairbanks and was considered moderate to high severity. Fire history records, which date to 1940, indicate that no other fires have burned the study plots since 1940 (Alaska Fire Service 2016). Discontinuous permafrost is found 40 to 50 cm below the soil surface, but ridgetops and upper south-facing slopes are often permafrost-free (Viereck and Dyrness 1979). *A. viridis* mostly occurs as an individual large shrub (Viereck and Little 2007) comprised of one or more tightly clustered ramets (or stems). *A. viridis* also grows as a small tree (~ 7 m) or in large patches (multiple individuals in close proximity to one another) on south-facing hills and mesic to subxeric valley lowlands. *A. viridis* density is relatively high in disturbed soils close to trails or roads.

Field and Laboratory Methods

Alder Distribution

Alder density was measured using the point-centered quarter (PCQ) method (Cottam and Curtis 1956) in the Wickersham Dome Fire (WDF) and Boundary Fire (BF). Sites were spaced 200 m apart along randomly located toposequence transects [Wickersham Dome Fire (n = 21 transects, n = 80 sites), Boundary Fire (n = 40 transects, n = 183 sites)], which were placed within the range of topographic variation sampled in the Wickersham Dome Fire (324 to 581 m elevation, 0 to 360° aspect, and 0 to 26° slope). In each quarter at each site we measured the distance (m) to nearest alder individual followed by the diameter (cm), average height (m), live or dead status, and number of all ramets for that individual alder. We define an "individual" alder as one or more tightly clustered ramets spatially separated from another individual. Nearest alder search distance was truncated to 50 meters.

Vegetation Types and Environmental Variables

Dominant plant cover was estimated at each site using the Braun-Blanquet relevé method for a 50-m radius circular plot (7854 m^2) (Mueller-Dombois and Ellenberg 1974; van der Maarel 1979). We identified trees and shrubs to species, grasses and forbs to genus, and all non-vascular plants as “moss” or “lichen,” except *Sphagnum* sp., which is identified to genus. Slope, aspect, elevation, and solar radiation data were averaged across a plot using a digital elevation model and Spatial Analyst toolbox in ArcGIS (ESRI 2014). Fire severity was averaged for each plot within the Boundary Fire using the difference in normalized burn ratio (dNBR) (U.S. Geological Survey and the U.S. Forest Service, 2014). Fire severity was not determined for the Wickersham Dome Fire plots due to a lack of pre-fire satellite imagery. Pre-fire dominant

vegetation type for the Boundary Fire was determined by the proportion of burned trees (standing and down) and unburned canopy-dominant trees, and subsequently verified using pre-fire satellite imagery (May 2002 Landsat 7 ETM image).

N-fixation and Nodule Biomass

Vegetation types were defined via a hierarchical cluster analysis of the relevé plot data (analysis described below), and N-fixation sampling was stratified by burn scar, vegetation type, and day of year. From June 29th to July 29th, 2015 - the period of peak N-fixation (Uliassi and Ruess 2002, Anderson et al. 2004) - we sampled 48 alders among 19 plots across four vegetation types in the BF, and 48 alders among 21 plots across three vegetation types in the WDF. At each plot, N-fixation rates were sampled from one to four plants of average growth and health - one experimental sample per plant and one control sample per plot. N-fixation rate was measured using a $^{15}N_2$ uptake method (Anderson et al. 2004, Ruess et al. 2009, Ruess et al. 2013) (Appendix 1.A). Determination of nodule-level N-fixation rate (μmole N g nodule^{-1} hr^{-1}) followed previous calculations (Anderson et al. 2004) and accounts for the fixation of both $^{15}N_2$ and $^{14}N_2$.

Between July 30th and September 28th, 2015, plant-level nodule biomass (g nodule m^{-2} plant^{-1}) was sampled at each plot that had been sampled for nodule-level N-fixation rate. Five alder plants of representative size and health were randomly selected, and for each plant five soil cores were taken at random within the area of nodulation - a 1 m buffer around the perimeter of each alder plant that is assumed to have a uniform distribution of nodules. Each core included the organic soil horizon and top 5 cm of the mineral horizon. Cores from a single plant were pooled (in a Ziplock® bag) and transported to the lab. Soil cores were rinsed through a sieve, and

nodules were sorted by live or dead status. Nodules were then dried at 65 °C to constant mass and weighed to the nearest 0.1 mg. Plant-level live nodule biomass is expressed as g nodule m^{-2} $plant^{-1}$ by scaling total live dry nodule mass to the area cored (118.8 cm^2) around each plant (Ruess et al. 2009, Ruess et al. 2013).

Soil and Leaf

Organic soil depth was measured at ten locations along a 20-m transect that bisected a randomly chosen, representative alder at each N-fixation plot. One of the ten soil depth locations was randomly selected for Oi, Oe, and Oa depth measurements as well as a mineral soil sample approximately 5 cm below the organic horizon. Bulk density (g cm^{-3}), soil pH, total N (% N), carbon (C) (% C) and phosphorus (P) (% P) were all measured from the mineral soil sample following Mitchell and Ruess (2009a). Beneath each alder that was sampled for N-fixation, organic soil moisture (%) and temperature (°C) were measured with a CS620 HydroSense water-content probe (Campbell Scientific, Logan, UT, USA) and a TM99A REOTEMP digital thermometer (REOTEMP Instruments, San Diego, CA, USA), respectively. Measurements were taken at 10 random locations and the probes were inserted to the same depth at which nodules were located. For these same plants, a leaf punch (7.07 cm^2) was taken from each of 10 leaves and punches were pooled into one sample. Leaf samples were dried at 40 °C until reaching constant mass and then weighed to the nearest 0.1 mg. Specific leaf mass (mg cm^{-2}) was calculated for each plant as the leaf sample dry weight divided by the leaf sample area.

Vegetation Classification

Post-fire vegetation types were determined for each burn scar by hierarchical clustering of plot-level plant species cover estimates in PC-ORD, Version 5.0 using Euclidean distance measures and Warde's linkage method (McCune and Mefford 1999). Any species occurring in less than 5% of all plots was removed from the dataset before relativizing species cover. Indicator Species Analysis (ISA) in PC-ORD (Dufrêne and Legendre 1997) was used to identify which hierarchical grouping configuration produced the most distinct vegetation types for each burn scar. For all grouping configurations between a 2-group and a 15-group configuration, the p-values of all significant indicator species were averaged and the grouping configuration with the lowest average p-value was chosen (Dufrêne and Legendre 1997).

Alder Growth Traits (Density, Growth, and N-input)

After sampling alder density using the PCQ method, we decided Siberian alder populations were non-randomly aggregated instead of completely spatially random. Therefore, we calculated alder density using the distance to nearest alder at each PCQ site and a nonparametric estimator of density (Patil et al. 1979; Patil et al. 1982; Mitchell 2010) implemented by the function *np.density.est* (Mitchell 2010) in program R (R Core Team 2016). A nonparametric median test in SPSS (IBM Corp 2010) was used to identify significant differences in nearest alder distance (alder density) by post-fire age (11 vs 44 years) and among vegetation types within each burn scar.

The alder growth variables - plant-level live nodule biomass (g nodule m^{-2} $plant^{-1}$), plant-level dead nodule biomass (g nodule m^{-2} $plant^{-1}$), average ramet height (m), specific leaf mass (mg cm^{-2}), mean ramet diameter (cm), and the number of live and dead ramets - were

intercorrelated ($P < 0.05$, $|r| > 0.3$). Therefore, we conducted a principal component analysis (PCA) in SPSS (IBM Corp 2010) to assess growth using the 2015 plots ($n = 40$) as the sampling units. The KMO Measure of Sampling Adequacy and Bartlett's test of sphericity were used to test each variable's sample size and whether or not the matrix was an identity matrix.

Since N-fixation rates are assumed to be constant over a 24-hour period (R.W. Ruess, unpublished data), we multiplied nodule-level N-fixation rate (μmol N g^{-1} hr^{-1}) by plant-level live nodule biomass (g nodule m^{-2} $plant^{-1}$) and converted the product to a daily rate. A seasonality step function (Uliassi and Ruess 2002, Anderson et al. 2004, Ruess et al. 2009) was used to convert daily plant-level N-fixation inputs (g N m^{-2} $plant^{-1}$ day^{-1}) into annual plant-level N-fixation inputs (g N m^{-2} $plant^{-1}$ yr^{-1}). Values of annual plant-level N-fixation input represent the average amount of N input immediately adjacent to a single alder, in a single year. To estimate annual stand-level N-fixation inputs (kg N ha^{-1} yr^{-1}), we multiplied the average area of nodulation for a plot (m^2 $plant^{-1}$) (previously described) by annual plant-level N-fixation input (g N m^{-2} $plant^{-1}$ yr^{-1}) and alder density (plants ha^{-1}). Values of annual stand-level N-fixation input represent the total amount of N input by an alder population within a given stand in a single year.

AICc Models

Alder density (distance to nearest alder), growth (PCA axes), plant-level live nodule biomass, nodule-level N-fixation, and annual plant-level N-fixation input were modeled separately via multiple linear regression and AICc best models subset multi-model inference. Predictors included environmental characteristics, post-fire age (regional-scale only), and fire severity (Boundary Fire only). Normalized predictors were tested for a marginally significant correlation with the response (Pearson's, $P < 0.1$) and marginally significant predictors were

included in the global model. Collinear predictors were sequentially removed from the global model starting with those of weakest correlation to the response (and of relatively low ecological information) until none of the predictor variables were highly collinear ($|r| < 0.6$). Post-fire age was forced into all regional global models and fire severity (dNBR) was forced into all Boundary Fire global models. Separate global models were created for each response variable at the regional scale (across both burn scars) and for each burn scar (n = 12 global models). The *dredge* function within the *MuMIn* package of R (Barton 2016) was used to detect the best model subsets (AICc $\leq$ 2 units of lowest AICc) within each global model. The β coefficient for each parameter within a best model subset of a global model was standardized by partial standard deviation (Cade 2015) and then averaged across all of the best model subsets using the function *model.avg* from the package *MuMIn* (Barton 2016). The result was a ranking of important environmental characteristics (topoedaphic) that control alder density, growth (PCA1 and PCA2), plant-level live nodule biomass, nodule-level N-fixation rate and annual plant-level N-input across the region and within each burn scar.

Structural Equation Models

Structural equation models (SEM) were used to test for direct and indirect effects of fire severity and topoedaphic variables on alder density, growth, and N-fixation in the Boundary Fire. SEM predictors included in the significant AICc best subsets predictors and fire severity. Models were fit using the *lavaan* package in R (Rosseel 2012). Non-significant ($P > 0.05$) variables in the SEM models were sequentially removed until only significant predictors remained. Modification indices were used to identify ecologically significant missing paths that were not initially included in the AICc best models subset (Grace et al. 2012). SEM model

fitness was determined using the chi-square test (*P* values > 0.05), the root mean square error of approximation (RMSEA; lower 90% confidence intervals of RMSE close to zero), and the comparative fit index (CFI > 0.9) (Grace et al. 2012).

Statistical Analysis

Unless stated otherwise, all tests of statistical significance were determined at $\alpha = 0.05$ using *Rcmdr* (Fox 2005) in the program R (R Core Team 2016). The Shapiro-Wilk test was used to assess the normality of predictor variables, and non-normal variables were transformed using the Box-Cox power transformation in R. Homogeneity of variance across factor levels of categorical variables was checked with Levene's test. One-way ANOVAs were used to test for differences in alder growth traits between burn scars and among vegetation types. For significant ANOVA results, Tukey's test of honest significant difference was implemented to identify factor level differences. For non-normal variables, differences were checked with the Kruskal-Wallis test and the Dunn-Bonferroni post-hoc test. Descriptive statistics throughout the text are untransformed and express as the mean ± 1 standard error, except alder density (plants ha^{-1}) and alder annual stand-level N-fixation inputs (kg N ha^{-1} yr^{-1}), which are both reported as mean ± 1 standard deviation.

RESULTS

Vegetation Classification

Hierarchical clustering and indicator species analysis resulted in three distinct post-fire vegetation types for the Wickersham Dome Fire that were named according to the post-fire

dominant tree species within in each type: Black Spruce, Deciduous, and Mixed (black spruce and deciduous codominance) (Table 1.1). In the Boundary Fire, four post-fire vegetation types emerged and were named according to their dominant indicator species and level of fire severity: Deciduous-Moderate, Black Spruce-Moderate to High, Black Spruce-Moderate, and a pre-fire Black Spruce-High (Table 1.1). Given the lack of strong indicator species for the Black Spruce-High vegetation type, it was instead named according to the dominant pre-fire vegetation type – black spruce.

Alder Growth Traits

N-fixation

The mean nodule-level N-fixation rate of the younger Boundary Fire (12.88 ± 1.18 µmol N g^{-1} hr^{-1}) was 70% higher than in the Wickersham Dome Fire (7.58 ± 0.59 µmol N g^{-1} hr^{-1}) ($P < 0.05$), (Figure 1.2a). Within the Wickersham Dome Fire, nodule-level N-fixation in the Black Spruce vegetation type (5.85 ± 1.04 µmol N g^{-1} hr^{-1}) was 22% lower than the Deciduous ($P = 0.433$) and 37% lower than the Mixed ($P < 0.05$) vegetation types (7.52 ± 0.43 and 9.34 ± 0.77 µmol N g^{-1} hr^{-1}, respectively) (Figure 1.2a). Within the Boundary Fire, there were no differences in nodule-level N-fixation rate among the post-fire Black Spruce vegetation types, or between the Deciduous-Moderate type and any of the Black Spruce types ($P > 0.05$); however, within-vegetation type standard errors were much greater than was the case in the Wickersham Dome Fire (Figure 1.2a).

We could not detect a significant difference ($P < 0.05$) in plant-level live nodule biomass between the Boundary Fire (16.30 ± 3.56 g nodule m^{-2} $plant^{-1}$) and the Wickersham Dome Fire (9.45 ± 1.58 g nodule m^{-2} $plant^{-1}$), nor among vegetation types within either burn scar (Figure

1.2b), likely due to the large amount of variance within vegetation types and between burn scars. Moreover, because areas of nodulation (m^2 $plant^{-1}$) differed between burn scars and among vegetation types (data not shown), but are not incorporated into estimates of plant-level live nodule biomass (g nodule m^{-2} $plant^{-1}$), our values likely do not reflect differences in the absolute amount of live nodule biomass per plant (g $plant^{-1}$) between these two burn scars.

The units of annual plant-level N-fixation input do not account for differences in the total area around a plant that is likely to have nodules - the area of nodulation - and therefore are relative rather than absolute estimates of annual plant-level N-fixation input. Annual plant-level N-fixation input in the Boundary Fire (6.86 ± 1.65 g N m^{-2} $plant^{-1}$ yr^{-1}) was nearly two times higher ($P < 0.05$) than the Wickersham Dome Fire (2.26 ± 0.03 g N m^{-2} $plant^{-1}$ yr^{-1}) (Figure 1.2c), suggesting that fire generally increases plant-level N-fixation input. Within the Wickersham Dome Fire, annual plant-level N-fixation input varied by vegetation type - the Black Spruce vegetation type (1.16 ± 0.07 g N m^{-2} $plant^{-1}$ yr^{-1}) was 63% and 61% lower ($P < 0.05$) than the Deciduous and Mixed types (3.17 ± 0.04 and 3.00 ± 0.07 g N m^{-2} $plant^{-1}$ yr^{-1}, respectively) (Figure 1.2c). There were no differences in annual plant-level N-fixation input among vegetation types of the Boundary Fire ($P > 0.05$), including the three burn severity types that were black spruce dominated (Figure 1.2c). This lack of difference across vegetation types of the Boundary Fire suggests that fire may have homogenized the expected environmental variability among vegetation types that otherwise would account for strong differences in annual plant-level N-fixation. As a result, all vegetation types of the Boundary Fire expressed higher amounts of live nodule biomass (and subsequently annual plant-level N-fixation inputs) compared to the Wickersham Dome Fire. In considering the lack of difference across vegetation types of an early-age burn scar (Boundary Fire), coupled with the difference in plant-level N-

fixation input among vegetation types of the older Wickersham Dome Fire it appears that annual plant-level N-fixation inputs in post-fire black spruce decreases more than in any other vegetation type, as time since fire increases.

Alder Density

Alder density varied by post-fire age and fire severity, as well as by vegetation types within each burn scar (Figure 1.2d). Alder density in the younger Boundary Fire (65 ± 14 plants ha^{-1}) was 150% lower ($P < 0.05$) than the Wickersham Dome Fire (162 ± 39 plants ha^{-1}) (Figure 1.2d). The magnitude of this difference was driven by very low alder density in the Black Spruce-High severity vegetation type of the Boundary Fire (2 ± 1 plant ha^{-1}) (Figure 1.2d), which had 97% ($P < 0.05$) lower alder density than the Black Spruce-Moderate and Black Spruce-Moderate to High fire severity vegetation types (59 ± 27 and 61 ± 20 plants ha^{-1}, respectively), and 99% lower ($P < 0.05$) density than the Deciduous-Moderate vegetation type in the Boundary Fire (164 ± 44 plants $^{-1}$) (Figure 1.2d). The Black Spruce-Moderate and Black Spruce-Moderate to High types did not differ from one another by alder density ($P > 0.05$) (Figure 1.2d). Within the Wickersham Dome Fire, alder density of the Black Spruce vegetation type (98 ± 34 plants ha^{-1}) was 34% and 50% lower than the Deciduous and Mixed vegetation types, respectively (154 ± 53 and 195 ± 74 plants ha^{-1}), but these differences were not significant ($P > 0.05$) (Figure 1.2d).

Stand-level N-fixation Input

To estimate annual stand-level fixation inputs, annual plant-level N-fixation input was multiplied by alder density and area of nodulation. Though the Boundary Fire had higher annual plant-level N-fixation input than the Wickersham Dome Fire ($P < 0.05$), lower plant density

compared to the Wickersham Dome Fire ($P < 0.05$) resulted in comparable rates ($P > 0.05$) of annual stand-level N-fixation inputs between these two burn scars (2.75 ± 0.08 and 2.91 ± 0.06 kg N ha^{-1} yr^{-1}, respectively) (Figure 1.2e). Annual stand-level N-fixation inputs in the black spruce vegetation type of the Wickersham Dome Fire were 82% lower than in the deciduous vegetation type ($P < 0.05$) (Figure 1.2e). Similarly, within the Boundary Fire, the black spruce vegetation types' average annual stand-level N-fixation inputs were 92% lower than in the deciduous type of the Boundary Fire (Figure 1.2e). Strong differences in annual stand-level N-fixation inputs between deciduous and black spruce dominated vegetation types suggest that both annual stand-level N-fixation inputs and vegetation type dynamics are controlled by similar environmental factors. Among the black spruce plots in the Boundary Fire, the Black Spruce-High vegetation type annual stand-level N-fixation inputs were, on average, 88% lower than the Black Spruce-Moderate and Black Spruce-Moderate to High vegetation type N-inputs (Figure 1.2e), suggesting that fire severity can limit annual stand-level N-fixation inputs (via reductions in alder density).

Alder Growth

The PCA of alder growth variables resulted in two significant axes that explained 48% and 26% of alder growth, respectively (Table 1.2). Alder plant-level live nodule biomass (+), average ramet height (+), mean ramet diameter (+) and specific leaf mass (-) loaded on the first PCA axis (hereafter referred to as *PCA1*). The number of live and dead ramets per plant loaded positively onto the second PCA axis (hereafter referred to as *PCA2)*. Dead nodule biomass was excluded from the PCA due to insufficient sample size (KMO < 0.5).

Higher values of PCA1 indicate plots with alders that were relatively tall, with greater basal diameter, thinner leaves, and more plant-level live nodule biomass than alders on plots of lower PCA1 values (Figure 1.3). Across the region, the Boundary Fire and the Wickersham Dome Fire did not have significantly different ($P = 0.71$) values of PCA1 (-0.06 ± 0.23 and 0.06 ± 0.12, respectively) (Figure 1.3a) (Appendix 1.B). Deciduous-dominated vegetation types had significantly higher PCA1 values ($P < 0.05$) than black spruce dominated vegetation types in the Boundary Fire (Deciduous-Moderate versus Black Spruce-Moderate) (Figure 1.3b) (Appendix 1.C) and the Wickersham Dome Fire (Deciduous versus Black Spruce) (Figure 1.3b) (Appendix 1.C, Appendix 1.D).

Higher values of PCA2 indicate plots with alders that had more ramets (live and dead) per plant than alders on plots of lower PCA2 values (Figure 1.3a). PCA2 was higher in the Wickersham Dome Fire (0.46 ± 0.24) than in the Boundary Fire (-0.51 ± 0.12) ($P < 0.05$) (Figure 1.3a) (Appendix 1.B), which likely reflects alder's characteristic sprouting of additional ramets as it ages. PCA2 did not vary significantly among vegetation types within the Boundary Fire (Appendix 1.C) or among vegetation types within the Wickersham Dome Fire ($P = 0.498$ and P

= 0.642, respectively) (Appendix 1.D) (Figure 1.3b) suggesting that alder ramet production is not controlled by the same environmental factors which define a vegetation type.

Modeling Alder Growth Traits

AICc best subsets were used to model alder density, growth (PCA1 and PCA2), plant-level live nodule biomass, nodule-level N-fixation rate and annual plant-level N-fixation inputs regionally (across both burn scars) and within each burn scar using topoedaphic environmental characteristics, post-fire age (regional models only), and fire severity (dNBR) (Boundary Fire models only) as predictors. In the Boundary Fire, we used SEM to further analyze the relative importance (direct and indirect effects) of fire severity versus environmental variables on the aforementioned alder response variables.

Alder Density

Regionally, plots with high organic soil moisture ($\beta = -6.68$) were associated with lower alder density ($P < 0.05$) (Table 1.3). Within the Boundary Fire, alder density was highest in plots that had relatively deeper Oe horizons ($\beta = 5.55$) ($P < 0.05$) (Table 1.3). Across all plots in the Boundary Fire ($n = 19$), the SEM did not reveal any significant effects of fire severity on alder density directly or indirectly ($P > 0.05$), however a SEM for black spruce plots in the Boundary Fire ($n = 11$) revealed a significant indirect negative effect of fire severity on alder density (Figure 1.4a). Conversely, variation in alder density across all stands of the Wickersham Dome Fire seems largely driven by organic soil moisture ($\beta = -9.83$) and slope ($\beta = 7.30$) ($P < 0.05$); wet or shallow-sloped plots (valley-bottoms and ridgetops) had lower alder density than drier or steeper-sloped plots (hillsides) (Table 1.3). These results indicate that at the Wickersham Dome

Fire, alder density is directly controlled by environmental characteristics (e.g. organic soil moisture and slope position). At the regional scale, across both burn scars, alder density was controlled by an interaction between fire severity effects that determine alder distribution patterns immediately after a fire, and environmental characteristic effects that inhibit or enhance the spread of alder populations as post-fire age increases.

Alder Growth

Regionally, PCA1 was highest in plots of low O horizon depth ($\beta = -0.64$) and low Oe depth ($\beta = -0.29$) (Table 1.3, Figure 1.3b); yet, within the Boundary Fire higher mineral soil pH ($\beta = 0.39$) and low organic soil moisture ($\beta = -0.31$) were additional predictors of high PCA1 values ($P < 0.05$) (Table 1.3, Figure 1.3c). SEM models for black spruce plots at the Boundary Fire ($n = 11$) revealed a direct negative effect of fire severity on PCA1, but likely a net positive effect of fire severity on PCA1 through its negative effects on O horizon depth (Figure 1.4b). In contrast, PCA1 in the Wickersham Dome Fire was singularly controlled by O horizon depth ($\beta = -0.58$) within the AICc model ($P < 0.05$) (Table 1.3). Although, post-fire age had no effect on PCA1 regionally ($P > 0.05$) (Table 1.3); differences in which variables predicted PCA1 across both burn scars suggest that mineral soil pH and organic soil moisture may interact with post-fire age.

PCA2 (an index of live and dead ramets), was strongly controlled by post-fire age ($\beta = 0.43$) and organic soil moisture ($\beta = -0.28$) at the regional level ($P < 0.05$) (Table 1.3 and Figure 1.3b). Within the younger Boundary Fire, higher elevation ($\beta = 0.34$) and higher soil pH ($\beta = 0.29$) were both positively correlated with a greater PCA2 ($P < 0.05$) (Table 1.3, Figure 1.3c).

Within the Wickersham Dome Fire, however, PCA2 was best predicted by an inverse relationship with mineral soil C:N ratio ($\beta = -0.58$) ($P < 0.05$) (Table 1.3, Figure 1.3d).

These results indicate that during early stand development following a fire (Boundary Fire), alder plants grow many large ramets and have greater plant-level live nodule biomass on well-drained plots with shallower O horizon depth, lower organic soil moisture, and higher mineral soil pH (Figure 1.3c); yet, higher severity fires limit alder growth on black spruce plots (Figure 1.4b). Later in post-secondary succession (Wickersham Dome Fire) alder grows best (taller, wider, and more numerous ramets and nodules) in the shallowest O horizons, especially where mineral soil C:N ratios are low (Figure 1.3d).

Alder N-fixation

Across the region, O horizon depth ($\beta = -2.16$) and post-fire age ($\beta = -2.02$) were the strongest predictors of annual plant-level N-fixation input ($P < 0.05$) (Table 1.3). The components of annual plant-level N-fixation input, which are nodule-level N-fixation rate and plant-level live nodule biomass, were separately controlled by post-fire age ($\beta = -2.68$) and O horizon depth ($\beta = -7.08$), respectively, at the regional scale ($P < 0.05$) (Table 1.3). Within the younger Boundary Fire, alders growing in shallow organic horizons with low mineral soil N:P ($\beta = -3.55$) ($P < 0.05$) and C:N ratios ($\beta = -2.37$) ($P < 0.1$) had the highest annual plant-level N-fixation input – a result largely due to the significantly higher plant-level live nodule biomass in shallow organic soils ($\beta = -8.08$) with low mineral soil N:P ($\beta = -6.41$) ($P < 0.05$) and marginally significant higher rates of nodule-level N-fixation where mineral soil C:N ratios ($\beta = -2.37$) ($P < 0.1$) were low (Table 1.3). A SEM of plant-level N-fixation input for Black spruce plots in the Boundary Fire ($n = 11$) (Figure 1.4c) revealed that fire severity had a direct negative effect on

organic soil depth and therefore an indirect positive effect on live nodule biomass; thus high fire severity indirectly increased plant-level N-fixation input in the Boundary Fire (Figure 1.4c). Conversely, within the Wickersham Dome Fire, alder at lower elevations had lower annual plant-level N-fixation input ($\beta = 0.77$) ($P < 0.1$) – a result driven by lower nodule-level N-fixation rates at the lowest elevation plots (valley bottoms) ($\beta = 1.90$; $P < 0.05$; Table 1.3). Taken together, the controls over alder annual plant-level N-fixation input seem to interact across spatiotemporal scales. Local plot conditions (e.g. soil chemistry and O horizon depth) control annual plant-level N-fixation input in early-age post-fire secondary succession while broader-scale landscape variables (e.g. topography) become the dominant controls over annual plant-level N-fixation input in intermediate-age post-fire secondary succession.

Variation of Controls on Alder Growth Traits

Differences in alder growth (PCA1 and PCA2) for the Boundary Fire were controlled by a mixture of variables that were significantly different ($P < 0.05$) between deciduous and black spruce vegetation types (O horizon depth and organic soil moisture) as well as variables that did not vary significantly ($P > 0.05$) by vegetation type (mineral soil pH, elevation, and mineral soil N:P ratios) (Appendix 1.E). Nodule-level N-fixation in the Boundary Fire was not controlled by any variable measured in this study, nor did it vary across vegetation types (Table 1.3, Figure 1.2). One of the controls over alder density in the Boundary Fire (Oe depth) did not vary by vegetation type, but an indirect control (fire severity) was significantly higher in the Black Spruce-High and Black Spruce-Moderate to High vegetation types compared to the Deciduous-Moderate and Black Spruce-Moderate types (Appendix 1.E). Within the Wickersham Dome Fire, alder growth and N-fixation were only controlled by variables that were significantly

different ($P < 0.05$) between the deciduous and black spruce vegetation types (O horizon depth, mineral soil C:N ratio, and elevation) (Appendix 1.F). The controls of alder density in the Wickersham Dome Fire (organic soil moisture and slope) did not vary significantly by vegetation type (Appendix 1.F).

DISCUSSION

Spatiotemporal Variation in Alder Growth Traits

Environmental characteristics, fire severity and post-fire age differentially affect alder distribution and growth traits. Patterns of variation in alder density, growth, plant-level live nodule biomass, nodule-level N-fixation rate and annual plant-level N-fixation inputs are dependent on the spatiotemporal extent of observation (post-fire age and vegetation type). Describing differences in alder growth traits between an early- and intermediate-aged burn scar within the same ecoregion, and across a fire severity gradient within a single burn scar, will help to disentangle the overall effects of fire severity, post-fire age, and vegetation type on alder growth traits and subsequent effects on total ecosystem N.

While annual plant-level N-fixation inputs (g N m^{-2} $plant^{-1}$ yr^{-1}) cannot be directly scaled to the stand level without incorporating alder density and total area of nodulation, it is useful to consider occurrences of high-density patches of Siberian alder (e.g. 1 plant m^{-2}) - particularly when comparing deciduous versus black spruce vegetation types. We can express patch-scale inputs of N in units traditionally used at the landscape scale (kg N ha^{-1} yr^{-1}). Accordingly, a theoretical 1 ha patch of alder in the Deciduous-Moderate vegetation type of the Boundary Fire would fix approximately 91 ± 30 kg N yr^{-1}, whereas the same size patch of alder in the Black Spruce-Moderate vegetation type would input approximately 33 ± 31 kg N yr^{-1}. Strong differences in N-input between alder patches of these two vegetation types are due to the substantially (though non-significant) higher live nodule biomass in the Deciduous-Moderate vegetation type. Patch-scale calculations indicate that Siberian alder can fix N at rates comparable to thin-leaf alder (*A. tenufolia*) of boreal forest floodplains (Van Cleve et al. 1971,

Uliassi and Ruess 2002, Anderson et al. 2004, Ruess et al. 2013). Yet, because high-density patches of Siberian alder are less frequent than thin-leaf alder, Siberian alder stand-level N-fixation inputs are still lower than stands of floodplain forest that contain thin-leaf alder. Our results do, however, highlight the fact that Siberian alder N-inputs in the boreal forest are much more abundant than previously thought (DeLuca et al. 2002). Additionally, Siberian alder N-inputs to total N pools, while low in black spruce stands that burned at high severity, are relatively equal to bryophyte N-inputs (2 kg ha^{-1} yr^{-1}) in early-successional moderate-to-high severity stands, and are much higher in moderately burned deciduous stand types compared to bryophyte contributions.

Our study is the first to estimate total nodule biomass per alder plant using an assumed area of nodulation around the plant and then combine those estimates with nodule-level N-fixation and a robust measure of stand-level alder density to approximate stand-level N-fixation inputs for multiple stand types. Alder nodulation has been documented several meters away from individual plants (personal observation), and so our estimates of plant-level (and by extension, stand-level) Siberian alder N-fixation input are likely conservative. Given the importance of scaling nodule biomass to the plant-scale and then to the stand-scale, Siberian alder patch-scale N-input in past studies may have been underestimated (Anderson et al. 2004, Mitchell and Ruess 2009a) and therefore its contributions to stand-level N pools may have been underestimated.

Effect of Fire Severity on N-input

In boreal Alaska, there is abundant evidence that fire severity, pre- and post-fire vegetation, organic horizon depth, and topoedaphic conditions are linked (Duffy et al. 2007,

Walker et al. 2016). Our data suggest there is also a connection between fire severity and alder growth traits within the black spruce vegetation type. Fire severity indirectly decreased alder density upon increased combustion of the O horizon. In the boreal forests of Sweden, Schimmel and Granstrom (1996) found that initial rhizomatous-shrub bud-bank mortality was higher with increasing depth of a burn. The reduction in alder density after extreme fire may be due to the destruction of alder rhizomes that are predominately found in the Oe layer of deep O horizons in the black spruce forest (personal observation), which has been shown in other studies of fire and alder (Zasada 1986). Lantz et al. (2010) showed that increased fire severity could improve seedbeds and the productivity of alder on burned sites. However, extreme fire severity has been known to eliminate rhizomatous shrubs for several years post-fire (Schimmel and Granstrom, 1996) as well as eliminate alder seed banks (Zasada et al. 1983); thus significantly lower alder density in high severity black spruce stands 11 years after the Boundary Fire may indicate a shift towards reductions of alder density in these stands. High fire severity did, however, positively influence plant-level live nodule biomass through reductions of the O horizon (Figure 1.4c). Reductions of the O horizon in thick black spruce organic mats likely coincided with increased available P (Kutiel and Shaviv 1988, Certini 2005), which increased nodule growth (Uliassi and Ruess 2002, Anderson et al. 2004, Ruess et al. 2013). Additionally, reductions in soil moisture, increased soil temperature, and an increase of soil area that maintains optimal oxygen concentrations all likely benefited nodule growth (MacConnell 1959, Anderson et al. 2004). Soil moisture and temperature were measured at the site of collected nodules (i.e. where nodulation is optimal in the soil layer) instead of deeper down in the organic or mineral soil where values of soil temperature and moisture are much more likely to fluctuate across stand types. As a result, we were unable to detect a clearer response of nodules to moisture and temperature. Regardless

of the causes of increased nodulation in high-severity, black spruce fire scars, drastic reductions in alder density overwhelmed the increase in plant-level live nodule biomass resulting in reductions of Siberian alder N-inputs compared to more moderately burned black spruce stands (Figure 1.2) – a reduction that may persist throughout post-fire secondary succession without aggressive alder propagation. The results of this study outline a possible threshold in the fire-alder relationship beyond which extreme fire severity can effectively lower Siberian alder N-inputs.

Disentangling Fire, Vegetation Type, and Abiotic Effects on Alder Growth Traits

We disentangled the effects of fire, vegetation type, and abiotic factors on alder growth traits by examining patterns of alder growth traits as well as the controls over alder growth traits across vegetation types. An analysis of these interactions in post-fire secondary succession revealed that fire may initially reduce the differences in alder density, growth and nodule-level N-fixation rate between deciduous and black spruce vegetation types. However, as early post-fire succession progresses into intermediate-age succession, environmental controls (O horizon depth and soil moisture) likely begin to dominate over the initial fire effects, leading to strong differences in growth and nodule-level N-fixation between the deciduous and black spruce vegetation types. The controls over alder density do not vary by vegetation type in intermediate-age succession where alder populations vigorously add new individuals regardless of stand type. These results concur with others who have found Siberian alder density does not vary by stand type (Mitchell and Ruess 2009b), but rather variation in plot-level burn severity and soil moisture dominate over stand-type environmental characteristics as the principal factors controlling Siberian alder's seemingly random distribution (Figure 1.4, Table 1.3).

Post-fire N-loss and Recovery

Estimates of total N pools (tree canopy and soil organic layer N) within interior black-spruce forest vary from 702 kg N ha^{-1} (Van cleve et al. 1983b) to 1754 kg N ha^{-1} (Boby et al. 2010). According to Boby et al. (2010), an average of 900 kg N ha^{-1} (canopy and soil N) was volatized in upland black spruce forest fires of 2004. The average post-fire Siberian alder N-input within black spruce stands of this study (0.86 ± 0.03 kg N ha^{-1} yr^{-1}) combined with estimates of atmospheric deposition and feathermoss N-fixation (0.3 kg N ha^{-1} yr^{-1} and 2 kg N ha^{-1} yr^{-1}, respectively) (DeLuca et al. 2002, Gundale et al. 2011) would offset the 2004 average combustion losses of N after 285 years of post-fire secondary succession. The moderate to high severity black spruce stands of this study showed much higher N-input rates of 1.99 kg N ha^{-1} yr^{-1}, and when combined with N deposition and feathermoss fixation, would offset N combustion losses within 210 years. Van Cleve et al. (1983b) estimated that a mature upland aspen (*Populus tremuloides* Michx.) stand (55 yrs old) and birch (*Betula neoalaskana* Sarg.) stand (77 yrs old) of the Alaskan interior contained 909 and 1070 kg N ha^{-1}, respectively. Black spruce stands in this study that experienced high severity fire and were subsequently dominated by deciduous seedlings post-fire, had Siberian alder N-input rates that averaged 0.06 ± 0.003 kg N ha^{-1} yr^{-1}. At these rates, Siberian alder N-input would contribute a total of 130 and 182 kg N ha^{-1} over 55 to 77 years of secondary succession to aspen and birch stands, respectively. Since high fire severity black spruce stands lose roughly 1400 kg N ha^{-1} through combustion (Boby et al. 2010), the N input rates of this study hardly offset N losses due to fire. Furthermore, these rates would not supply enough N to build a mature deciduous forest 55 to 77 years post-fire, per Van Cleve et al. (1983b) N stand-level N estimates. Boby et al. (2010) observed an increasing loss of N through

combustion as fire severity increased. Our study results show a pattern of low N-input in moderately burned black spruce, high N-input for moderate to high severity burned sites, and low N-input in extremely high severity sites. High severity fire can dramatically reduce stocks of N in black spruce forests (Body et al. 2010) while converting stands to a deciduous trajectory that has severely limited Siberian alder N-input and therefore total N-recovery during deciduous stand development. Mineral soil N does not change significantly between immediate post-fire levels and later stages of secondary succession in the boreal forest (Brais et al. 2000, Palviainen et al. 2017), and N mineralization is typically not a major source of N-input into this system (Högberg et al. 2017), therefore it is unlikely that mineral soil N-mineralization could make up for low Siberian alder N-input after high severity fire. Furthermore, our estimates of N-recovery do not account for N-leaching, which is about 13% of total N-inputs for N-limited boreal forests (Palviainen et al. 2017). Therefore, it is unlikely that N lost due to volatilization would be offset by N-inputs within the time periods that we estimate.

Landscape-scale Alder N-input and Ecological Impacts

These results highlight differences in Siberian alder N-input among vegetation types, landscape positions, fire severity levels, and differently aged burn scars. This study does not account for differences in the total amount of area covered by each vegetation type within each burn scar. To understand better how fire severity and post-fire age may alter stand type and therefore landscape-level Siberian alder total N-input, stand-level results must be mapped within the entire Boundary Fire and Wickersham Dome Fire scars. Additionally, stand-level N-fixation inputs do not address the within-stand spatial distribution of alder N-input, which is specifically dependent on the spatial distribution of alder plants (e.g. clumped versus dispersed) within a

stand. Conducting a spatial analysis of alder patch distribution within stand types and mapping the results at the landscape scale would further increase the resolution of landscape-scale Siberian alder N-input and thus the spatially explicit effects of alder N-fixation on ecosystem processes.

Conclusions

We hypothesized that increased fire severity in the boreal forest directly reduces Siberian alder stand-level N-fixation inputs due to reductions of alder density. Our results showed fire increases nodule-level N-fixation regardless of severity, while alder density responds positively to moderate fire severity, and the combined result is higher Siberian alder N-input after a moderate fire. Yet high fire severity likely destroys alder populations in black spruce stands, which offsets nodule-level N-fixation increases to effectively reduce overall N-inputs. Fire also has the effect of dissolving differences in nodule-level N-fixation between deciduous and black spruce stands, with nodules from both stand types fixing substantial amounts of nitrogen, but those effects do not persist through intermediate succession as nodule-level N-fixation rates in black spruce stands fall faster than in deciduous stands. High severity fire in black spruce stands involves the highest loss of N (Boby et al. 2010) but also the lowest post-fire Siberian alder N-inputs. Because these high-severity stands typically convert from black spruce to deciduous dominance, Siberian alder N-inputs can neither offset losses of N nor supply enough N for deciduous stand growth. Though the effects of fire on Siberian alder N-input are strong, defining the nature of that relationship at the landscape-level will require accurate mapping of the area occupied by each pre- and post-fire stand type.

FIGURES

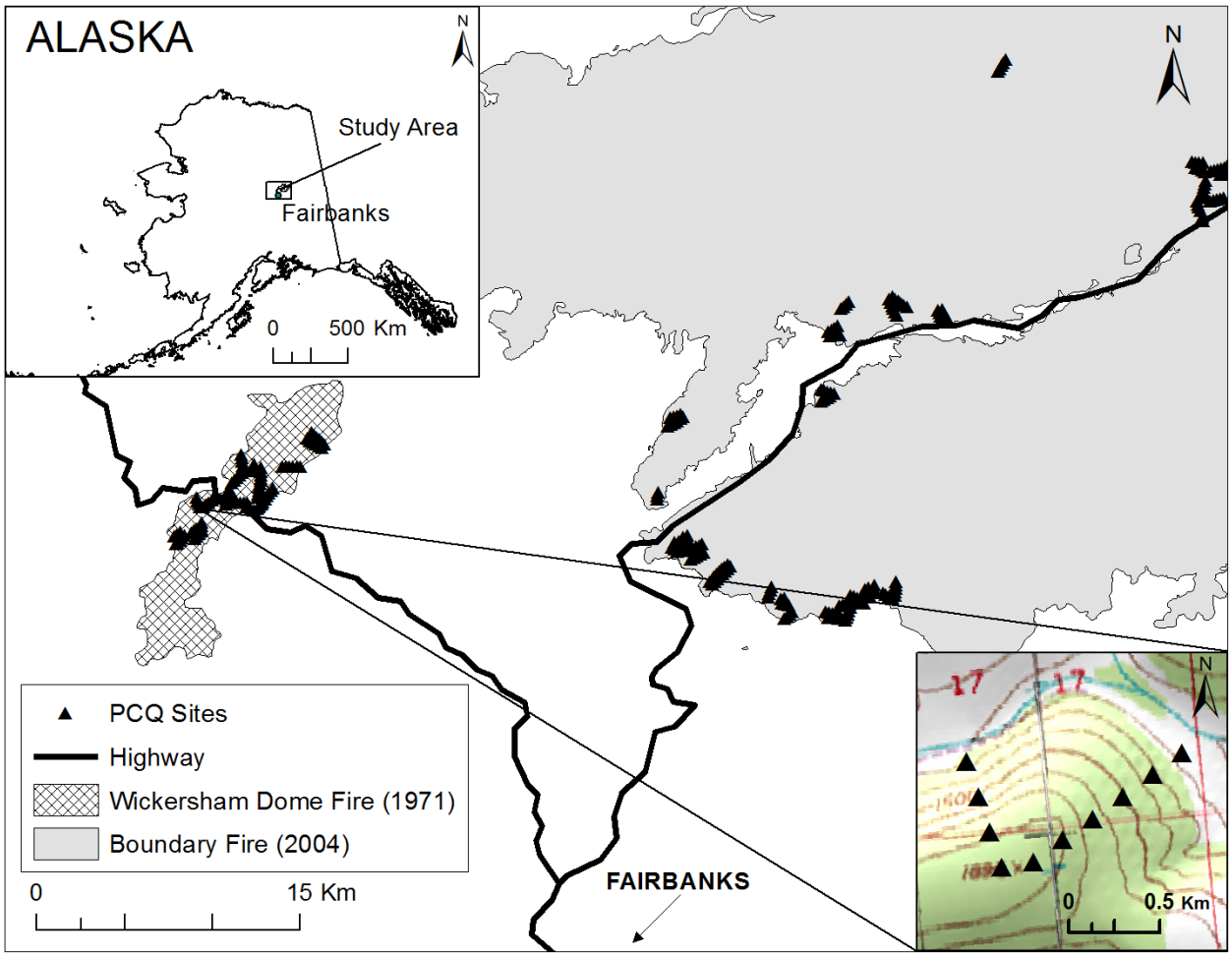

Figure 1.1. The Boundary Fire area (grey) and the Wickersham Dome Fire (hashed lines), located approximately 35 km north of Fairbanks, Alaska. Topographic inset depicts the typical layout of PCQ sites and transects.

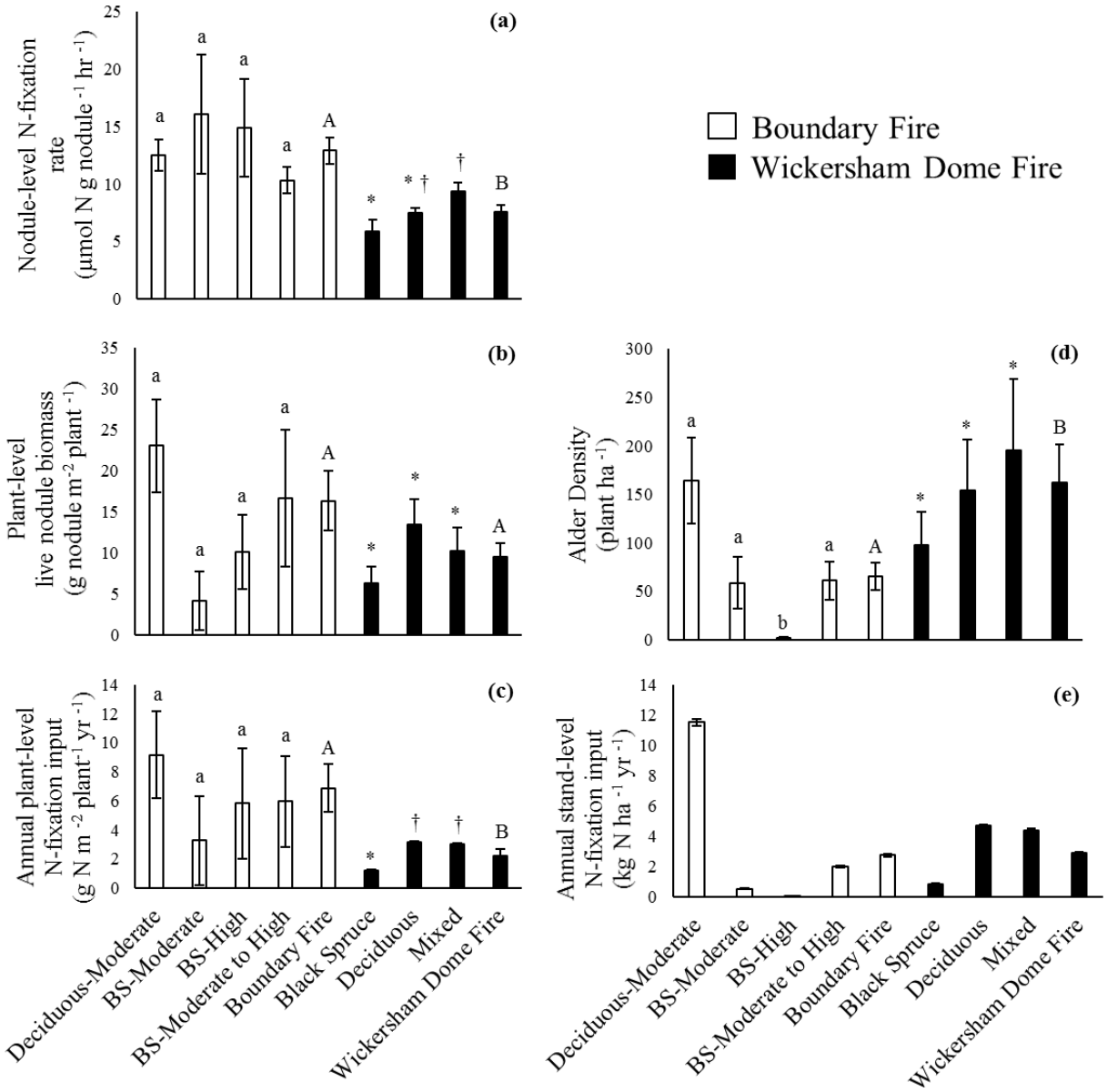

Figure 1.2. Alder population structure by study area (n = 40), Boundary Fire (n=19), Wickersham Dome Fire (n=21), and by vegetation types within each burn scar. Values on x-axis represent a vegetation type or an entire burn scar. The Boundary Fire and its vegetation types are not shaded. The Wickersham Dome Fire and its vegetation types are shaded black. On the x-axis, BS = black spruce. Significant differences are determined at $P < 0.05$ level between burn scars (A or B), among vegetation types of the Boundary Fire (a or b), and vegetation types among the Wickersham Dome Fire (* or †). I did not test for significant differences among all vegetation types across both burn scars. Significant differences in stand-level N-fixation inputs could not be tested. Values are mean + 1 SE, except for density and stand-level N-fixation input which are both mean + 1 SD.

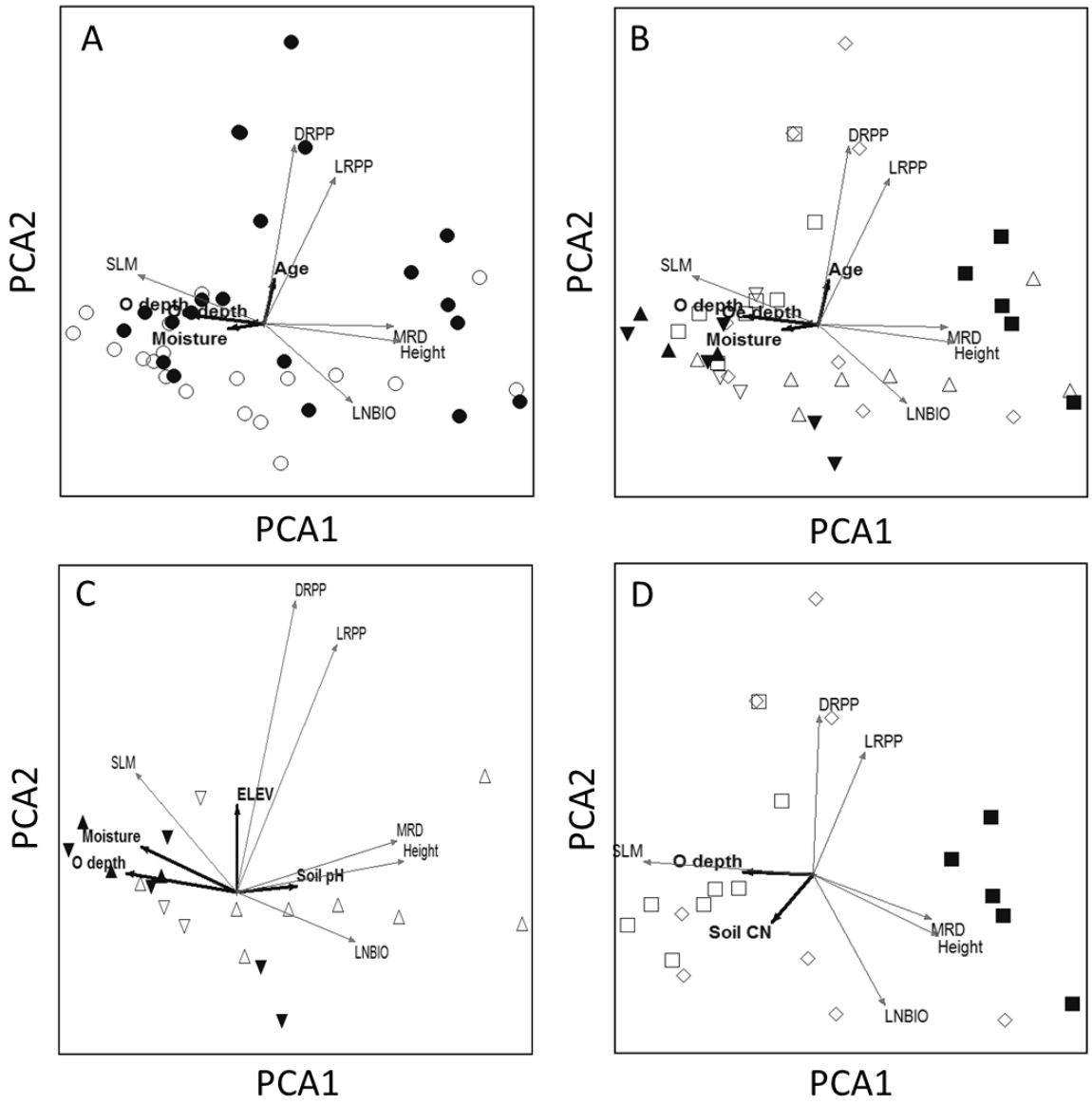

Figure 1.3. Principal component analysis (PCA) of alder growth variables: plant-level live nodule biomass (NODBIO), average height (Height), mean ramet diameter (MRD), specific leaf mass (SLM), live ramets per plant (LRPP), and dead ramets per plant (DRPP). Thin grey lines represent the alder growth variables used in the PCA and their orientation to PCA1 and PCA2. Thick black lines represent the important predictor variables of each PCA axes, for each scale, as determined by AICc best subsets modeling. ELEV = elevation, Moisture = organic soil moisture, O depth = organic horizon depth, Oe depth = Oe horizon depth, Age = post-fire age, Soil pH = mineral soil pH, Soil CN = mineral soil C:N ratio. PCA1 and PCA2 at the regional-scale with sites A) categorized by burn scar and B) all vegetation types, and vegetation types by burn scar (C = Boundary Fire, D = Wickersham Dome Fire). Symbols: graph A (○ = Boundary Fire, ● = Wickersham Dome Fire), graph B and C (△ = Deciduous-Moderate, ▲= Black Spruce-Moderate, ▽ = Black Spruce-High, ▼ = Black Spruce-Moderate to High), graph B and D (□ = Black Spruce ■ = Deciduous, ◊ = Mixed).

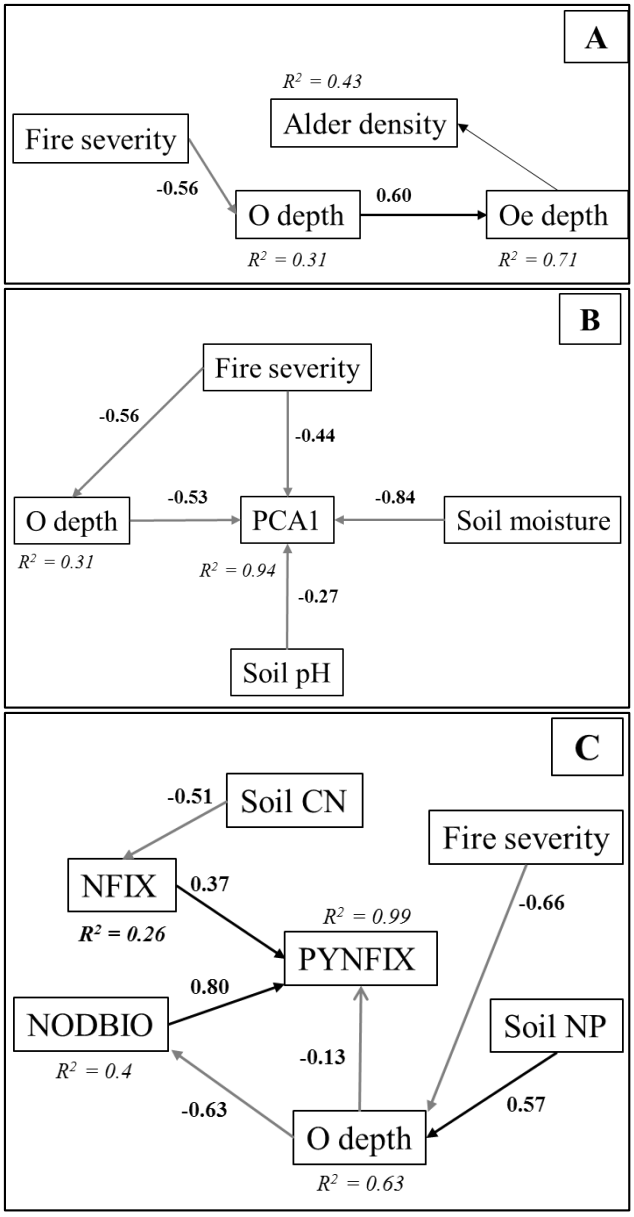

Figure 1.4. Structural equation model of A) alder density (plants ha^{-1}), B) PCA1, and C) PYNFIX (annual plant-level N-fixation input (g N m^{-2} $plant^{-1}$ yr^{-1})) in post-fire black spruce plots of the Boundary Fire (n = 11). Fire severity = difference in normalized burn ratio (dNBR), O depth = depth of the organic soil horizon (cm), Oe depth = depth of the hemic layer of the O soil horizon (cm), Soil pH = pH of mineral soil horizon, Soil moisture = moisture of the organic horizon at the depth which alder nodules were located (%), Soil CN = mineral soil C:N ratio, NFIX = nodule-level N-fixation rate (µmol N g $nodule^{-1}$ hr^{-1}), NODBIO = plant live nodule biomass (g nodule m^{-2} $plant^{-1}$), Soil NP = mineral soil N:P ratio. Standardized beta coefficients are shown for predictor variable pathways. Negative pathways are symbolized gray and positive pathways are black. R^2 values are included for the response variables.

TABLES

Table 1.1. Vegetation types sampled in the Wickersham Dome Fire and the Boundary Fire. Cut-offs for dNBR values are low (25 to 275), moderate (276 to 549), and high (≥ 550), and different letters indicate significant differences ($P < 0.05$). Indicator species (and cover classes) are listed in order of descending indicator value. Values for difference in normalized burn ratio (dNBR) reflect the mean ± standard error, while different letters reflect significant differences between or among vegetation types.

Vegetation Type	**dNBR**	**Indicator species (and cover classes)**
Wickersham Dome Fire		
Black Spruce	NA	Moss, *Rhododendron groenlandicum, Vaccinium vitis-idaea, Picea mariana* (seedling), *Betula glandulosa, Sphagnum* sp., *Equisetum* sp., *Eriophorum* sp., *Rubus chamaemorus, Polygonum alpinum, Rhododendron palustre* ssp. *decumbens*
Deciduous	NA	Litter, *Betula neoalaskana* (tree), *Populus tremuloides* (tree), dead and down trees, *Populus tremuloides* (seedling), *Rosa acicularis, Geocaulon lividum, Picea glauca* (tree)
Mixed	NA	Lichen, *Picea mariana* (tree), *Vaccinium uliginosum, Salix* sp., *Cornus canadensis, Empetrum nigrum*
Boundary Fire		

Table 1.1 cont.

Deciduous-Moderate	354 ± 30 a	*Betula neoalaskana* (tree), *Betula neoalaskana* (seedling), litter, *Calamagrostis* sp., dead and down trees, *Populus tremuloides* (seedling), *Chamerion angustifolium*, *Rubus idaeus*, *Cornus canadensis*, *Populus tremuloides* (tree), *Rosa acicularis*, *Lycopodium* sp.
Black Spruce-Moderate	350 ± 35 a	*Sphagnum* sp., *Rubus chamaemorus*, *Picea mariana* (tree), Lichen, *Rhododendron palustre* ssp. *decumbens*, *Eriophorum* sp., *Vaccinium vitis-idaea*, *Picea mariana* (seedling), *Vaccinium oxycoccos*, Moss, *Betula nana*, *Empetrum nigrum*, *Andromeda polifolia*, *Polygonum alpinum*, *Petasites frigidus*
Black Spruce-High	664 ± 28 c	*Salix* sp. and *Carex* sp.
Black Spruce-Moderate to High	499 ± 28 d	*Vaccinium uliginosum*, *Rhododendron groenlandicum*, *Betula glandulosa*, *Betula* sp. (hybrid shrub), *Arctogrostis latifolia*

Table 1.2. Total variance explained by a principal component analysis (PCA) of alder growth variables (plant-level live nodule biomass (g nodule m^{-2} $plant^{-1}$), average ramet height (m), specific leaf mass (g cm^{-2}), mean ramet diameter (cm), and a count of live and dead ramets per plant) across all plots nodule-level N-fixation rate plots (n = 40). Eigenvalue cutoff was set at 1.

	Initial Eigenvalues			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
Axis	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	2.895	48.257	48.257	2.895	48.257	48.257	2.761	46.017	46.017
2	1.534	25.561	73.818	1.534	25.561	73.818	1.668	27.802	73.818
3	.707	11.777	85.595						
4	.397	6.622	92.217						
5	.305	5.083	97.300						
6	.162	2.700	100.000						

Table 1.3. AICc model predictors for alder density (plants ha^{-1}), growth (PCA1 and PCA2), plant-level live nodule biomass (g nodule m^{-2} $plant^{-1}$), nodule-level N-fixation rate (µmol N g^{-1} hr^{-1}), and annual plant-level N-fixation input (g N m^{-2} $plant^{-1}$ yr^{-1}) across the region (n = 40), Boundary Fire (n = 19), and Wickersham Dome Fire (n = 21). Standardized beta coefficients and importance values are in parentheses, respectively, for each predictor variable. The baseline level for post-fire age was set as the Boundary Fire.

Response	Predictor(s) (standardized beta coefficient, importance value)
REGION	
Alder density	**Organic soil moisture (-6.68, 1) ***, mineral soil C:N (-3.05, 0.38)
PCA1	**O horizon depth (-0.64, 1) *, Oe depth (-0.29, 1) ***, *mineral soil N:P ratio (-0.21, 0.52)†*, postfire age (0.19, 0.52), mineral soil pH (0.14, 0.13)
PCA2	**Postfire age (0.43, 1)*, organic soil moisture (-0.28, 0.84)*,** *mineral soil C:N ratio (-0.27, 0.51)†*, mineral soil P (-0.19, 0.16), mineral soil bulk density (0.18, 0.14)
Plant-level live nodule biomass	**O horizon depth (-7.08, 1)*,** postfire age (-2.27, 0.46)
Nodule-level N-fixation rate	**Postfire age (-2.68, 1)***
Annual plant-level N-fixation input	**O horizon depth (-2.16, 1)*, postfire age (-2.02, 1)*,** soil N:P ratio (-1.24, 0.56), Oe depth (-0.89, 0.37)
BOUNDARY FIRE	
Alder density	**Oe depth (5.55, 0.77)***, *Oa depth (-3.26, 0.50)†, dNBR (-2.97, 0.47)†*

Table 1.3 cont.

PCA1	**O horizon depth (-0.49, 0.99)*, mineral soil pH (0.39, 0.95)*, organic soil moisture (-0.31, 0.82)***
PCA2	**Elevation (0.34, 0.99)*, mineral soil pH (0.29, 0.96)***
Plant-level live nodule biomass	**O horizon depth (-8.08, 0.82)*, mineral soil N:P (-6.41, 0.61)*,** *organic soil moisture (-5.69, 0.33)†, mineral soil pH (5.05, 0.15)†,* slope (-4.74, 0.12)
Nodule-level N-fixation rate	*Mineral soil C:N ratio (-2.37, 0.52)†,* slope (-1.98, 0.47), dNBR (1.76, 0.34), mineral soil bulk density (1.82, 0.18)
Annual plant-level N-fixation input	**Mineral soil N:P ratio (-3.55, 0.78)*, O horizon depth (-3.08, 0.78)*,** *slope (-2.77, 0.22)†*
WICKERSHAM DOME FIRE	
Alder density	**Organic soil moisture (-9.83, 0.94)*, slope (7.30, 0.74)***
PCA1	**O horizon depth (-0.59, 0.94)***
PCA2	**Mineral soil C:N ratio (-0.58, 1)***, organic soil moisture (-0.34, 0.5)
Plant-level live nodule biomass	NA

Nodule-level N-fixation rate	**Elevation (1.90, 1)***

Table 1.3 cont.

Annual plant-level N-fixation input	*Elevation (0.77, 0.69)†*, O horizon depth (-0.67, 0.54)

* Significant predictors ($P < 0.05$) are in bold print.
† Marginally significant predictors ($P < 0.1$) are italicized.

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APPENDICES

Appendix 1.A. Nodule biomass and N-fixation methods.

Nodule samples were excavated from the organic horizon and at the interface of organic and mineral soil horizons adjacent to the central ramet of individual alders. Approximately 1 gram of live nodule was cut from the root and placed in a 60 ml polyethylene syringe containing 50 ml of ambient air. Exactly 10 ml of 99 atom % $^{15}N_2$ gas was injected into the incubation syringe, and the syringe was placed into undisturbed organic soil at the same depth from which the nodules were extracted. After a ten-minute incubation period, nodules were cleaned of root and soil, rinsed with deionized water, and placed into a 4-ml cryovial, which was immediately frozen and stored in liquid N_2 during transfer from the field to the lab. A control nodule sample was collected from each plant, but not incubated, and was used to determine natural ^{15}N abundance. In the laboratory, experimental and control nodule samples were oven-dried, pulverized, and analyzed on a Sercon stable isotope mass spectrometer (Sercon Limited, Crewe, Cheshire, UK) for both total N and ^{15}N content (atom% ^{15}N).

Appendix 1.B. Descriptive statistics for alder growth variables across the region. Statistics were calculated from the 2015 dataset (n = 40) unless stated otherwise (2014 dataset, n=200). Significant differences between the Boundary Fire and Wickersham Dome Fire are determined at $P < 0.05$ level and shown in bold font. Statistics are calculated for plots which had alder. lnbio = live nodule biomass (g nodule m^{-2} $plant^{-1}$); dnbio = dead nodule biomass (g nodule m^{-2} $plant^{-1}$); SLM = specific leaf mass (mg cm^{-2}); MRD = mean ramet diameter (cm); lrpp = live ramets per plant; drpp = dead ramets per plant; PCA 1 = first principal component axis; PCA 2 = second principal component axis. Values reflect mean ± the standard error.

Variable	BF	WDF	ANOVA, Kruskal Wallis, or Median Test
lnbio	16.3 ± 3.6	9.5 ± 1.6	$F(1,38) = 0.777$, $p = 0.384$
dnbio	8.4 ± 2.6	5.5 ± 1.8	χ^2 (2, N = 40) = 0.060, p = 0.807
SLM	6.9 ± 0.3	6.7 ± 0.3	$F(1,38) = 0.244$, $p = 0.625$
MRD (n = 200)	**2 ± 0**	**3 ± 0**	**χ^2 (1, N = 200) = 38.933, p = 4.386e-10**
lrpp (n = 200)	**7 ± 0**	**14 ± 1**	**F(1,198) = 36.04, p = 9.09e-09**
drpp (n = 200)	**1 ± 0**	**3 ± 0**	**χ^2 (1, N = 200) = 67.356, p = 2.267e-16**
PCA 1	-0.06 ± 0.23	0.06 ± 0.12	$F(1,38) = 0.143$, $p = 0.708$
PCA 2	**-0.51 ± 0.12**	**0.46 ± 0.24**	**χ^2 (1, N = 40) = 10.651, p = 0.0011**

Appendix 1.C. Descriptive statistics of the alder growth variables in the Boundary Fire. Statistics were calculated using the 2015 dataset (n = 19), unless stated otherwise (2014 dataset, n=125). Variables significantly different ($P < 0.05$) across vegetation types are shown in bold print. Different letters among columns in the same row indicate significant differences among vegetation types at $P < 0.05$. * Pairwise differences significant at $P < 0.05$. † Pairwise differences significant at $P < 0.1$. lnbio = live nodule biomass (g nodule m^{-2} $plant^{-1}$); dnbio = dead nodule biomass (g nodule m^{-2} $plant^{-1}$); avgHei = average height of an individual's ramets (m); SLM = specific leaf mass (mg cm^{-2}); MRD = mean ramet diameter (cm); lrpp = live ramets per plant; drpp = dead ramets per plant; PCA 1 = first principal component axis; PCA 2 = second principal component axis. Values reflect mean ± the standard error.

Variable	Deciduous-moderate	Black Spruce-moderate	Black Spruce-high	Black Spruce-moderate-to-high	ANOVA or Kruskal-Wallis Test
lnbio	23.01 ± 5.68 a	4.09 ± 3.58 a	10.09 ± 4.49 a	16.6 ± 8.38 a	$F(3,15) = 1.607$, $p = 0.230$
dnbio	12.15 ± 4.53 a	7.03 ± 6.82 a	8.85 ± 8.42 a	2.86 ± 2.6 a	$F(3,15) = 2.351$, $p = 0.113$
avgHei	2.25 ± 0.33 a	1.16 ± 0.11 a	1.67 ± 0.05 a	1.69 ± 0.21 a	$F(3,15) = 2.288$, $p = 0.120$
SLM	**5.82 ± 0.23 a**	**8.27 ± 0.6 b**	**7.47 ± 0.26 b**	**7.57 ± 0.49 b**	**$F(3,15) = 8.671$, $p = 0.001$**
MRD	*2.8 ± 0.4 a*	*1.3 ± 0.2 a*	*1.7 ± 0.2 a*	*1.5 ± 0.3 a*	*$F(3,15) = 3.125$, $p = 0.0573$*
lrpp	**12.2 ± 3 a**	**5.7 ± 0.7 ab**	**3.4 ± 0.8 b**	**4 ± 0.6 b**	**$F(3,15) = 4.809$, $p = 0.0153$**
drpp	0.8 ± 0.3 a	0.7 ± 0.2 a	1.3 ± 1.3 a	0.6 ± 0.4 a	$F(3,15) = 0.278$, $p = 0.84$
PCA 1	**0.67 ± 0.33 a**	**-1.04 ± 0.21 b**	**-0.5 ± 0.07 ab**	**-0.38 ± 0.38 ab**	**$F(3,15) = 4.421$, $p = 0.0204$**
PCA 2	-0.32 ± 0.22 a	-0.52 ± 0.1 a	-0.53 ± 0.35 a	-0.81 ± 0.21 a	$F(3,15) = 0.829$, $p = 0.498$

Appendix 1.D. Descriptive statistics of the alder growth variables in the Wickersham Dome Fire. Statistics were calculated using the 2015 dataset (n = 21). Variables significantly different ($P < 0.05$) across vegetation types are shown in bold print. Different letters in the same row indicate significant differences among vegetation types at $P < 0.05$. lnbio = live nodule biomass (g nodule m^{-2} $plant^{-1}$); dnbio = dead nodule biomass (g nodule m^{-2} $plant^{-1}$); avgHei = average height of an individual's ramets (m); SLM = specific leaf mass (mg cm^{-2}); MRD = mean ramet diameter (cm); lrpp = live ramets per plant; drpp = dead ramets per plant; PCA 1 = first principal component axis; PCA 2 = second principal component axis. Values reflect mean ± the standard error.

Variable	Black Spruce	Deciduous	Mixed	ANOVA, Kruskal-Wallis, or Median Test
lnbio (g m^{-2})	6.3 ± 2.03 a	13.35 ± 3.19 a	10.17 ± 2.84 a	F(2,18) = 1.622, p = 0.225
dnbio (g m^{-2})	*3.12 ± 1.53 a*	*12.88 ± 6.16 a*	*3.38 ± 1.81 a*	*F(2,18) = 3.093, p = 0.070*
avgHei (m)	**1.52 ± 0.13 a**	**3.65 ± 0.29 b**	**2.21 ± 0.42 a**	**F(2,18) = 8.277, p = 0.003**
SLM (mg cm^{-2})	**7.63 ± 0.21 a**	**4.98 ± 0.33 b**	**6.9 ± 0.51 a**	**F(2,18) = 10.362, p = 0.001**
MRD (cm)	**1.8 ± 0.1 a**	**4.4 ± 0.4 b**	**2.5 ± 0.2 c**	**F(2,18) = 22.87, p = 0.00001**
lrpp	11.9 ± 2 a	16.2 ± 2.9 a	14.8 ± 4.9 a	F(2,18) =0.52, p = 0.603
drpp	2.2 ± 0.7 a	2.5 ± 0.6 a	2.7 ± 1.2 a	F(2,18) = 0.198, p = 0.822
PCA 1	**-0.68 ± 0.09 a**	**1.42 ± 0.22 b**	**-0.06 ± 0.33 a**	**F(2,18) = 12.06, p = 0.0004**
PCA 2	0.25 ± 0.31 a	0.66 ± 0.26 a	0.55 ± 0.55 a	F(2,18) = 0.454, p = 0.642

Appendix 1.E. Boundary Fire environmental characteristics by vegetation type (Deciduous-moderate (n = 8), Black Spruce-moderate (n = 3), Black Spruce-high (n= 3), Black Spruce-moderate-to-high (n = 5)). Slope, elevation, solar radiation, and fire severity values were calculated using the 2014 dataset (Deciduous-moderate (n = 67), Black Spruce-moderate (n = 20), Black Spruce-high (n= 53), Black Spruce-moderate-to-high (n = 43)). Environmental characteristics with a significant ANOVA, Kruskal-Wallis, or Median test result ($P < 0.05$) are in bold print, while marginally significant test results ($P < 0.1$) are in italics. Different letters indicate significant pairwise differences among vegetation types ($P < 0.05$). A Median test was used to assess differences in fire severity (dNBR) by vegetation type. Values reflect mean ± the standard error.

Environmental Characteristic	**Deciduous-moderate**	**Black Spruce-moderate**	**Black Spruce-high**	**Black Spruce-moderate-to-high**	**ANOVA, Kruskal-Wallis, or Median Test**
Organic soil temperature (°C)	**10.3 ± 0.4 a**	**6.8 ± 1.0 b**	**8.7 ± 0.6 ab**	**8.8 ± 0.6 ab**	**F(3,15) = 5.838, p = 0.008**
Organic soil moisture (%)	**5 ± 1 a**	**12 ± 2 b**	**9 ± 1 ab**	**9 ± 2 ab**	**F(3,15) = 6.068, p = 0.006**
O depth (cm)	**9.4 ± 0.9 a**	**18.7 ± 2.4 b**	**12.8 ± 2.1 ab**	**17.3 ± 2.9 b**	**F(3,15) = 5.252, p = 0.011**
Oi depth (cm)	*2.1 ± 0.7 a*	*9.2 ± 4.4 a*	*1.0 ± 0.3 a*	*3.0 ± 0.7 a*	*F(3,14) = 2.687, p = 0.087*

Appendix 1.E. cont.

Oe depth (cm)	3.9 ± 0.4 a	5.2 ± 0.4 a	3.5 ± 1.7 a	8.2 ± 4.0 a	$\chi^2(3, N = 19) = 2.761, p = 0.430$
Oa depth (cm)	4.9 ± 0.7 a	6.2 ± 2.0 a	5.2 ± 0.4 a	7.2 ± 2.5 a	$F(3,15) = 0.154, p = 0.925$
Mineral soil bulk density ($g\ cm^{-3}$)	0.78 ± 0.10 a	0.98 ± 0.18 a	1.04 ± 0.09 a	0.61 ± 0.13 a	$F(3,15) = 1.957, p = 0.164$
Mineral soil N (%)	0.24 ± 0.08 a	0.23 ± 0.05 a	0.20 ± 0.02 a	0.59 ± 0.14 a	$F(3,15) = 1.930, p = 0.168$
Mineral soil C (%)	4.27 ± 1.48 a	3.92 ± 1.29 a	3.46 ± 0.32 a	13.36 ± 3.56 a	$F(3,15) = 2.321, p = 0.117$
Mineral soil P (%)	**0.06 ± 0.01 a**	**0.07 ± 0.004 ab**	**0.07 ± 0.01 ab**	**0.12 ± 0.02 b**	**$F(3,15) = 3.322, p = 0.049$**
Mineral soil pH	4.47 ± 0.14 a	4.42 ± 0.23 a	4.16 ± 0.03 a	4.08 ± 0.14 a	$F(3,15) = 1.566, p = 0.239$

Appendix 1.E cont.

Mineral soil C:N ratio	**17.76 ± 0.97 ab**	**16.28 ± 1.96 ab**	**17.48 ± 0.58 a**	**21.95 ± 1.48 a**	**F(3,15) = 3.374, p = 0.047**
Mineral soil N:P ratio	3.68 ± 0.61 a	3.21 ± 0.62 a	3.19 ± 0.67 a	4.67 ± 0.72 a	F(3,15) = 0.841, p = 0.492
Slope (°)	**12 ± 0.3 a**	**12 ± 1 ab**	**10 ± 1 b**	**11 ± 1 ab**	**χ^2(3, N = 181) = 10.025, p = 0.020**
Elevation (m)	464 ± 8 a	457 ± 18 a	472 ± 9 a	461 ± 12 a	χ^2(3, N=181) =1.074, p = 0.780
Solar radiation (WH m^{-2})	**649582 ± 5934 a**	**559367 ± 15615 b**	**601338 ± 9285 b**	**585728 ± 9321 b**	**χ^2(3, N = 181) = 40.136, p = 9.971e-09**
Fire severity (dNBR)	**354 ± 30 a**	**350 ± 35 a**	**664 ± 28 c**	**499 ± 28 d**	**χ^2(3, N = 181) = 53.795, p < 0.0001**
N-Fix Sampling Day of Year	*188 ± 2*	*196 ± 7*	*198 ± 4*	*198 ± 2*	*χ^2(3, N = 19) = 7.473, p = 0.058*

Appendix 1.F. Wickersham Dome Fire environmental characteristics by vegetation type (Black Spruce (n = 8), Deciduous (n = 5), Mixed (n = 8)). Slope, elevation, and solar radiation values were calculated using the 2014 dataset (Black Spruce (n = 28), Deciduous (n = 25), Mixed (n = 27)). Environmental characteristics with a significant ANOVA or Kruskal-Wallis test result ($P < 0.05$) are bolded; marginally significant ($P < 0.1$) ANOVA or Kruskal-Wallis test results are italicized. Different letters indicate significant pairwise differences among vegetation types ($P < 0.05$). Values reflect mean ± the standard error.

Environmental Characteristic	Black Spruce	Deciduous	Mixed	ANOVA or Kruskal-Wallis Test
Organic soil temperature (°C)	8.6 ± 1.2 a	8.5 ± 1.5 a	9.2 ± 0.8 a	$F(2,18) = 0.062$, $p = 0.940$
Organic soil moisture (%)	11 ± 4 a	4 ± 1 a	6 ± 1 a	$F(2,18) = 1.288$, $p = 0.300$
O depth (cm)	**20.8 ± 1.9 a**	**10 ± 1.1 b**	**12.9 ± 1.1 b**	**$F(2,18) = 15.368$, $p = 0.000$**
Oi depth (cm)	2.9 ± 0.7 a	2.6 ± 0.4 a	2.5 ± 0.5 a	$F(2,18) = 0.149$, $p = 0.862$
Oe depth (cm)	**8.3 ± 1.7 a**	**2.7 ± 0.7 b**	**4.1 ± 0.6 ab**	**$F(2,18) = 6.578$, $p = 0.007$**
Oa depth (cm)	*7.8 ± 1.4 a*	*4.1 ± 0.6 a*	*5.3 ± 0.6 a*	*$F(2,18) = 3.013$, $p = 0.074$*
Mineral soil bulk density (g cm^{-3})	**0.69 ± 0.08 a**	**1.22 ± 0.14 b**	**0.9 ± 0.12 ab**	**$F(2,18) = 5.349$, $p = 0.015$**
Mineral soil N (%)	**0.41 ± 0.13 a**	**0.11 ± 0.03 b**	**0.21 ± 0.04 ab**	**$F(2,18) = 6.960$, $p = 0.006$**
Mineral soil C (%)	**8.01 ± 2.60 a**	**1.83 ± 0.71 b**	**3.38 ± 0.78 ab**	**$F(2,18) = 7.859$, $p = 0.004$**
Mineral soil P (%)	*0.08 ± 0.01 a*	*0.05 ± 0.01 a*	*0.07 ± 0.01 a*	*$F(2,18) = 2.636$, $p = 0.099$*
Mineral soil pH	4.41 ± 0.16 a	4.39 ± 0.16 a	4.41 ± 0.25 a	$F(2,18) = 0.174$, $p = 0.841$

Appendix 1.F cont.

Mineral soil C:N ratio	**19.43 ± 0.69 a**	**14.89 ± 1.05 b**	**15.5 ± 1.09 b**	**F(2,18) = 6.785, p = 0.006**
Mineral soil N:P ratio	**4.42 ± 0.61 a**	**2.05 ± 0.42 b**	**2.85 ± 0.34 ab**	**F(2,18) =5.672, p = 0.012**
Slope (°)	10 ± 1 a	11 ± 1 a	9 ± 1 a	F(2,77) = 0.798, p = 0.454
Elevation (m)	**386 ± 8 a**	**441 ± 11 b**	**488 ± 12 c**	**χ^2(2, N = 80) = 32.510, p = 8.721e-08**
Solar radiation (WH m^{-2})	**592025 ± 10153 a**	**664332 ± 5970 b**	**629162 ± 11138 c**	**F(2,77) = 18.040, p = 3.76e-07**
N-Fix Sampling Day of Year	191 ± 4	198 ± 4	194 ± 3	F(2,18) = 0.914, p = 0.419

CHAPTER 2: PREDICTING POST-FIRE SIBERIAN ALDER DISTRIBUTION AND ASSOCIATED NITROGEN-FIXATION INPUTS IN UPLAND INTERIOR ALASKA[2]

Abstract

Siberian alder (*Alnus viridis ssp. fruticosa*) is ubiquitous across the boreal forest of interior Alaska and acts as a keystone species because of its symbiotic relationship with the N-fixing *Frankia* bacteria. Alternations to Siberian alder landscape-level N-input after wildfire (via changes in N-fixation rate, nodule biomass, or plant density) would likely have a significant impact on total ecosystem N balance and therefore several N-dependent ecosystem processes that affect post-fire stand development including: net primary production, organic soil decomposition, and rates of C storage. We quantified changes in annual landscape-level N-fixation input as a result of high fire severity and stand conversion within the 2004 Boundary Fire burn scar. Each pre-fire vegetation type area showed a net increase in total annual landscape-level N-fixation input (+33.33, +17.14, and +56.24 t N yr^{-1} for the Deciduous, Mixed, and Black Spruce vegetation types, respectively). Increased landscape-level Siberian alder N-input was largely due to high rates of Siberian alder stand-level N-fixation input (kg N ha^{-1} yr^{-1}) in deciduous stands, and the conversion of roughly one-third of pre-fire black spruce to post-fire deciduous. However, increases in Siberian alder N-input are spatially restricted to deciduous trajectory stands after moderate-to-high severity fire and they counter losses of Siberian alder N-input areas of black spruce stand self-replacement or deciduous stand trajectories that resulted

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from high severity fire in pre-fire black spruce. Fire severity and pre-fire vegetation type interact to control Siberian alder N-input and thus stand development as well as post-fire N recovery at the landscape scale. Our results highlight the direct effect of fire on an important ecosystem process at the landscape scale.

INTRODUCTION

Siberian alder (*Alnus viridis ssp. fruticosa*) is ubiquitous across the boreal forest of interior Alaska and acts as a keystone species because of its symbiotic relationship with the nitrogen (N) -fixing *Frankia* bacteria. Nitrogen is commonly the limiting element to plant production within the boreal forest ecosystem (Tamm 1990; Högberg et al. 2017). Several ecosystem processes are driven by high alder N contributions such as tree growth and productivity within deciduous-dominated stand types (Heilman 1966; Van Cleve et al. 1971, 1983; Wurtz 1995), high nitrate concentrations that influence primary production within salmon headwater streams (Shaftel et al. 2012), and enhanced N availability and accelerated N cycling within aquatic ecosystems (Hu et al. 2001). Substantial Siberian alder N-input within a continuous patch of alder has been documented in various stand types of post-fire secondary succession (Anderson et al. 2004; Mitchell and Ruess 2009; Chapter 1) and is a function of nodule-level N-fixation, root nodule biomass, and alder density. However, landscape-level Siberian alder density, root nodule biomass, and nodule-level N-fixation rates across the Yukon-Tanana upland ecoregion has not been determined; therefore, total Siberian alder N-input at this regional scale is unknown. Siberian alder growth traits (density, live nodule biomass, and nodule-level N-fixation) vary by stand from early to late post-fire succession wherein late-

successional mixed stands often have higher alder density than early-age post-fire stands (Mitchell and Ruess 2009). Additionally, intermediate-age deciduous and mixed stands have higher N-input than stands dominated by black spruce (*Picea mariana* (Mill.) BSP) because of higher alder density, nodule biomass, and nodule-level N-fixation (Chapter 1). Siberian alder is also known to occur as a dominant understory species throughout early to late secondary succession in the upland forests of interior Alaska (Mitchell and Ruess 2009). Given the strong correlations between alder growth traits, stand age, and stand type, approximating alder growth traits by stand type and stand age, and then mapping stand age and stand type at the landscape-level would provide an approximation of landscape-level Siberian alder N-input across the upland boreal forest.

Climate-induced increases to fire severity in the boreal forest can result in the combustion of material legacies (e.g. vegetation, soil organic matter, seed banks) as well as stand conversions from black spruce to deciduous-dominated stands (Johnstone et al. 2010; Mann et al. 2012; Turetsky et al. 2017). Siberian alder has been shown to colonize vigorously and quickly by seed after a high-severity fire (Mathews 1992; Lantz et al. 2010) and by resprouting meristems after a low severity fire (Gilbert and Payette 1982). Siberian alder N-input in pre-fire black spruce stands that show post-fire deciduous dominance depends heavily on the level of fire severity, wherein high fire severity is associated with significantly reduced N-input but moderate to high fire severity resulted in increased Siberian alder N-input (Chapter 1). Due to predicted shifts in stand-type trajectory following severe fire, as well as the detrimental effect of high-severity fire on Siberian alder density and associated N-input, predicting Siberian alder N-input at the landscape-level requires knowledge of the interaction between fire severity and post-fire stand type trajectory. Alterations to Siberian alder's landscape-level N-input after fire (via changes in

N-fixation rate, nodule biomass, or plant density) would likely have a significant impact on total ecosystem N balance and therefore several N-dependent ecosystem processes including net primary production, organic soil decomposition, and rates of C storage (Tateno and Chapin 1997; Hyvönen et al. 2008), N export to aquatic ecosystems (Compton et al. 2003; Shaftel et al. 2012), and the direction and rate of succession (Chapin et al. 1994).

Our primary goal was to determine how Siberian alder N-input varies across the Yukon-Tanana ecoregion (Nowacki et al. 2001) and how climate-induced alterations to the historic fire regime may disrupt Siberian alder material legacies (i.e. seeds and propagules) and associated Siberian alder N-contributions which are an integral component of ecosystem memory within these systems. By quantifying Siberian alder N-inputs in pre- and post-fire stand types, and the amount of landscape area (ha) occupied by these stand types within each pre-fire to post-fire pathway, we can estimate Siberian alder N input at the landscape scale and assess how it might be influenced by fire severity and stand type conversions. Estimates of stand-level N-fixation inputs (kg N ha^{-1} yr^{-1}) and their variation along biotic and abiotic gradients are discussed in Chapter 1; we use those same stand-level N-fixation inputs in our calculations of landscape-level N-fixation input.

We hypothesized that landscape-level N-fixation input by Siberian alder increases following a severe fire as a result of substantial portions of the landscape converting from black spruce to deciduous stands. We chose to estimate Siberian alder annual landscape-level N-fixation input across the 200,000 ha Boundary Fire in pre- to post-fire conversion or non-conversion pathways, with a special emphasis on the pre-fire black-spruce to post-fire deciduous conversion pathway that is predicted by increased fire severity. The Boundary Fire was among the most extreme fires recorded in Alaska and reflects the high-severity fire regime that is

predicted to result from climate change. Due to a lack of pre-Boundary Fire data, however, we substituted Siberian alder N-input estimates from stand types of the 44-year old Wickersham Dome Fire scar for similar pre-Boundary Fire stand types that existed before the Boundary Fire. Our objectives were to 1) create a supervised classification of pre- and post-fire vegetation types in a burn scar using Landsat 7 ETM+ and Landsat 8 OLI satellite imagery and ground-truthed, plot-based vegetation data, 2) attribute Siberian alder stand-level N-fixation inputs (kg N ha^{-1} yr^{-1}) (Chapter 1) to pre- and post-fire vegetation types in order to estimate total pre- and post-fire annual landscape-level N-fixation input (t N yr^{-1}) by vegetation type, and 3) quantify changes in annual landscape-level N-fixation input within the 2004 Boundary Fire burn scar as a result of high fire severity and stand conversion.

METHODS

Study Area

Our study area encompassed two burn perimeters in the Yukon-Tanana Uplands ecoregion north of Fairbanks, Alaska (Figure 2.1). The Wickersham Dome Fire, which burned 5,500 ha in 1971, is located approximately 35 km NW of Fairbanks (64.9° N, 147.9° W). The Boundary Fire burned over 210,000 ha in 2004 and is located approximately 40 km NE of Fairbanks. Fire history records for interior Alaska indicate that no fires burned our study plots other than the Wickersham Dome and Boundary Fires since at least the 1940s – when the Alaska Fire Service began recording fire perimeter data (Alaska Fire Service 2016). The lower severity Wickersham Dome Fire is representative of fires that occurred before recent warming trends across the circumpolar boreal forest triggered increases in fire severity. In contrast, the

Boundary Fire, a fire from the largest fire year on record, is a precursor to the fire regime expected under predicted climate scenarios: increased area burned (by fire and by year), shorter fire-return intervals, and greater burn severity. Due to a lack of pre-fire data on community-specific rates of alder N-fixation within the Boundary Fire burn perimeter, modeling Siberian alder N-input on the lower severity Wickersham Dome Fire and substituting those estimates for pre-Boundary Fire N-input allows for a quantitative estimate of the climate-induced changes that are expected across the upland boreal forest ecosystem.

The climate of interior Alaska is subarctic continental with warm summers (July mean of ±23 ºC) and cold winters (January mean of -27 ºC) (Alaska Climate Research Center 2016). The average annual precipitation (1981 to 2010) for Fairbanks is 274.6 mm (Wendler et al. 2016). These two burn perimeters share similar late and mid-succession plant communities, topography, and geology and both fall into the Yukon-Tanana Uplands ecoregion (Nowacki et al. 2001). Most of the region covered by these two burn perimeters is underlain by permafrost 40 to 50 cm below the surface, but ridgetops and upper south-facing slopes are often permafrost-free (Viereck and Dyrness 1979). Pre-fire vegetation types were dominated by black spruce with an understory of willow (*Salix scouleriana* [Barratt]), Siberian alder, Labrador tea (*Rhododendron groenlandicum* [Oeder]), bog blueberry (*Vaccinium uliginosum* L.), low-bush cranberry (*Vaccinium vitis-idea* [L.]), and prickly rose (*Rosa acicularis* [Lindl.]) shrubs (Viereck and Dyrness 1979). Mosses also made up a nearly continuous ground cover, including feather mosses and occasionally *Sphagnum*. Occasional quaking aspen (*Populus tremuloides* [Michx.]) or Alaska birch (*Betula neoalaskana* [Sarg.]) stands were found on subxeric to mesic south-facing slopes or ridge tops, and leaf litter dominated the ground cover in these deciduous stands.

Field and Lab Methods

Pre-fire Vegetation Types

We determined the pre-fire dominant vegetation type of each Boundary Fire plot but not the Wickersham Dome Fire plots due to the lack of pre-fire satellite imagery for the 1971 Wickersham Dome Fire. Since fires often kill but do not destroy the boles or larger branches of living trees in the boreal forest (Kasischke et al. 1995), we used the proportion of burned trees (standing and down) and unburned canopy-dominant trees by species to estimate pre-fire dominant vegetation type. If a tree species comprised $\geq$ 70% of all snags and unburned canopy-dominant trees on a plot, then the species was considered pre-fire dominant. Three different pre-fire dominant vegetation types were designated in the 2004 Boundary Fire based on the dominant tree cover before the fire: 1) Black Spruce, 2) Mixed (co-dominance of black spruce and deciduous), or 3) Deciduous (Alaska birch or trembling aspen).

Post-fire Vegetation Types and Fire Severity

Within both burn perimeters, dominant plant cover was estimated using the Braun-Blanquet relevé method for a 50 m radius circular plot (7854 m^2) (Mueller-Dombois and Ellenberg 1974; van der Maarel 1979). We identified post-fire vegetation types by performing a hierarchical clustering of plant species relevé plot data from the Boundary Fire (n = 183 plots) and the Wickersham Dome Fire (n = 80 plots) which is described in detail elsewhere (Chapter 1). There are three post-fire vegetation types in the Wickersham Dome Fire and they were named according to the mean dominant tree cover within each type: Black Spruce, Mixed (black spruce and Alaskan birch/aspen), and Deciduous (Alaskan birch/aspen) (Chapter 1). In the Boundary Fire, there were four post-fire vegetation types named according to their dominant indicator

species and level of fire severity: Deciduous-Moderate, Black Spruce-Moderate to High, Black Spruce-Moderate, and a pre-fire Black Spruce-High (Chapter 1). Given the lack of strong indicator species for the Black Spruce-High vegetation type, it was instead named according to the dominant pre-fire vegetation type – black spruce – and fire severity level (Chapter 1). Fire severity was determined for each plot within the Boundary Fire using the difference in normalized burn ratio (dNBR) (U.S. Geological Survey and the U.S. Forest Service, 2014), as determined from pre- and post-fire satellite imagery over the burn perimeter. All dNBR 30-m pixels within or majority-overlapping (> 50% of pixel area) a Boundary Fire plot (approximately 8 pixels) were averaged to determine a mean dNBR value for the plot. We averaged the mean dNBR values of all plots within a post-fire vegetation type to determine the mean fire severity of each post-fire vegetation type (Appendix 2.A). Fire severity was not determined for the 1971 Wickersham Dome Fire due to a lack of the requisite pre-fire satellite imagery.

Mapping Pre- and Post-fire Vegetation Types

We used the Spatial Analyst toolbox in ArcMap 10.3 (ESRI 2014), Landsat 8 OLI imagery, and Landsat 7 ETM+ imagery to perform a supervised classification of post-fire vegetation types in the Wickersham Dome Fire (n = 80 plots), and pre- and post-fire vegetation types in the Boundary Fire (n = 183 plots). Landsat 8 OLI and Landsat 7 ETM+ surface reflectance products were processed by U.S. Geological Survey and were cloud-free and had a cell resolution of 30 m. We selected spring and summer imagery for both burn perimeters to determine which season would offer the best differentiation of post-fire vegetation types. Spring images were taken one week after green-up (approx. mid-May) while summer images were taken during peak plant growth (mid-June). The red, near-infrared (NIR), and short-wave infrared

(SWIR) bands of each image date were combined to make a single composite image. We chose to use a composite of the red, NR, and SWIR bands because they are the three most uncorrelated bands and therefore maximize spectral information within the image. Then we combined the spring and summer images into a single composite image to help capture topographic influence since solar elevation is very different in May versus June. Also, combined spring and summer imagery helps capture two distinct phases of plant phenology (i.e. green-up and peak growth). All composite images were clipped to the component of the fire area bounded by the topographic constraints initially sampled in both burn perimeters (elevation (324 to 581 m), aspect (0 to 360°), and slope (0 to 26°)) (Chapter 1). Furthermore, a 50 m buffer around all creeks, rivers, streams, roads, trails, and developed areas was clipped from the images to avoid extrapolating the classification of vegetation types into vegetation types that were not sampled in this study (e.g. riparian plant communities). We were unable to estimate annual stand-level N-fixation inputs in these clipped exclusion zones due to a lack of representative plot data, and therefore maps of vegetation types and N-inputs contain blank spaces of "No Data" within a fire perimeter. All calculations of changing stand area or landscape N-inputs exclude the areas of "No Data" that are delineated in the maps. We performed a separate supervised classification of each composite image using the ground-truthed relevé vegetation plot data (post-fire veg types) or the dominant post-fire snag data (pre-fire veg types) and the maximum likelihood classifier in ArcMap 10.3. Approximately 80% of the plots were used to train a classification, while the remaining 20% served as test sites for an accuracy assessment of the classification. To determine each plot's vegetation type (as determined by the supervised classification), we used a majority rule function (e.g. if 6 of 8 pixels overlapping a plot were classified as deciduous then the plot was deemed deciduous).

Accuracy Assessment

We performed an accuracy assessment of each image classification by determining the producer's accuracy and user's accuracy for each vegetation type, and the overall accuracy and the kappa coefficient for an entire image classification (Congalton and Green 1999). Producer's accuracy is the measure of the error of omission (the total number of correctly classified pixels in a category divided by the total number of reference pixels in that category). User's accuracy measures the error of commission (the total number of correctly classified pixels in a category divided by the total number of pixels classified into that category) (Congalton and Green 1999). The kappa coefficient is the proportionate reduction in error of the classification compared with a random classification (Cohen 1960). The overall accuracy is the total of correctly classified sites divided by the total number of sites in the error matrix (Congalton 1991). The image classifications with the highest overall accuracy and highest kappa statistic were chosen for further analysis.

Analysis

Scaling N-input

Measurement of alder growth traits is described in Chapter 1 and those traits included alder density (plants ha^{-1}), growth (height (m)), count of live and dead ramets (ramets ha^{-1}), ramet diameter (cm), plant-level live nodule biomass (g nodule m^{-2} $plant^{-1}$), nodule-level N-fixation rate (µmol N g $nodule^{-1}$ hr^{-1}), annual plant-level N-fixation input (g N m^{-2} $plant^{-1}$ yr^{-1}), and annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}). Annual stand-level N-fixation input is a function of several alder growth traits (alder density, nodule-level N-fixation, and nodule

biomass) whose environmental controls across upland boreal forest stand types are discussed in Chapter 1. Values of annual stand-level N-fixation input represent the total amount of N input by Siberian alder within a given stand (a continuous area of homogenous vegetation type, such as a black spruce stand) in a single year - these values do not address the spatial distribution of N-inputs within a stand which is dependent on the spatial distribution of alder plants (e.g. clumped versus dispersed); however, the density of alder plants within the stand was estimated in Chapter 1. In this study, we have spatially bounded landscape-level N-fixation input to the area sampled in each burn perimeter. To calculate pre- and post-fire landscape-level N-fixation input in the Boundary Fire, we multiplied each stand's total area (ha) within the study area (as determined by supervised classification of satellite imagery) by its annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}) for each stand. We did not directly measure pre-Boundary Fire annual stand-level N-fixation input. However, given the similarities in landscape, topography, soils, vegetation and other ecological factors between the two fire perimeters, we assume that plots within the 44-year old Wickersham Dome Fire and pre-Boundary Fire annual stand-level N-fixation inputs were likely similar. Thus, we applied the Wickersham Dome Fire estimates of annual stand-level N-fixation input for each separate vegetation type to its correspondingly similar pre-Boundary Fire vegetation types (e.g. Deciduous ≈ Deciduous, Black Spruce ≈ Black Spruce, and Mixed ≈ Mixed), and then multiplied those estimates by the pre-Boundary Fire area for each vegetation type to arrive at pre-Boundary Fire annual landscape-level N-fixation input.

Stand Conversions and Changing Siberian Alder N-input

To determine the difference between pre- and post-Boundary Fire annual landscape-level N-fixation input (Δ t N yr^{-1}), we spatially overlaid the pre-and post-fire vegetation classifications

in ArcMap. Using the Combine tool in the Spatial Analyst toolbox, we calculated the amount of area that each post-fire vegetation type occupied within each pre-fire vegetation type to quantify how fire affected the distribution of vegetation types. We used the dNBR raster to exclude areas within the Boundary Fire study area that did not burn. Because the dNBR raster was created with a cloudy Landsat 7 ETM+ SLC-off image, additional portions of the study area are excluded in the calculation of changing N-inputs. Estimates of pre-fire annual stand-level N-fixation input for the Boundary Fire were based on Wickersham Dome Fire estimates of annual stand-level N-fixation input for Black Spruce, Mixed, and Deciduous vegetation types. We multiplied the area within each pre-fire to post-fire pathway by its pre- and post-fire annual stand-level N-fixation input to arrive at pre- and post-fire annual landscape-level N-fixation input. The change in annual landscape-level N-fixation input (Δ t N yr^{-1}) was calculated by subtracting the pre-fire annual landscape-level N-fixation input from the post-fire annual landscape-level N-fixation input for each pre-fire to post-fire pathway.

To more clearly related changes in Siberian alder N-input to changes in vegetation type, we defined each post-Boundary Fire vegetation type as black spruce, deciduous, or mixed dominance. According to the Alaska Vegetation Classification (Viereck et al. 1992), the post-fire Black Spruce-High vegetation type most closely resembled open, low willow scrub and aspen woodland communities and is therefore categorized as a deciduous vegetation type for analysis purposes (Appendix 2.A). Also, the Black Spruce-Moderate, Black Spruce-Moderate to High, and Deciduous-Moderate vegetation types most closely resembled black spruce, mixed, and deciduous vegetation types, respectively (Appendix 2.A). After relating pre- and post-Boundary Fire vegetation types, we chose to define a vegetation type conversion as an area that changed from one vegetation type before the fire to a characteristically different vegetation type

after the fire (e.g. pre-fire Deciduous to post-fire Black Spruce-Moderate (black spruce)). Conversely, we define a non-conversion as that area that was classified within the same vegetation type before the fire as after the fire (e.g. pre-fire Deciduous to post-fire Deciduous-Moderate (deciduous)).

RESULTS

Imagery Classification and Stand-level N-fixation Input

Wickersham Dome Fire vegetation types were classified and annual stand-level N-fixation inputs were directly attributed to their respective vegetation type (Figure 2.2). Within the Wickersham Dome Fire, the Black Spruce vegetation type, which had the lowest annual stand-level N-fixation input (0.83 ± 0.04 kg N ha^{-1} yr^{-1}), occurred along nearly every stream corridor and halfway up hillside backslopes, except those hillsides that were south-facing on which the high N-inputting Mixed or Deciduous vegetation types (4.40 ± 0.09 and 4.72 ± 0.02 kg N ha^{-1} yr^{-1}, respectively) dominated. The best classification of vegetation types for the Wickersham Dome Fire resulted in an overall accuracy and kappa coefficient of 75% and 63%, respectively (Table 2.1). The Deciduous vegetation type of the Wickersham Dome Fire had higher producer's accuracy than user's accuracy (100% and 83%, respectively), whereas the Black Spruce vegetation type had lower producer's accuracy than user's accuracy (67% and 80%, respectively) (Table 2.2). Accordingly, the Deciduous vegetation type was overestimated in the classification, i.e., pixels were incorrectly placed in the Deciduous class even though they were likely of a Black Spruce or Mixed vegetation type. Conversely, the Black Spruce vegetation type was underestimated in the classification – areas that were truly Black Spruce on

the ground were instead classified as Deciduous or Mixed on the map. The Mixed vegetation type was not very well classified (60% producer's and user's accuracy) which is likely due to strong spectral similarities between it and the Deciduous and Black Spruce vegetation types, especially during intermediate succession when black spruce and deciduous trees are co-dominant within the canopy.

Pre-Boundary Fire vegetation types were classified for the Boundary Fire perimeter (Figure 2.3); however, annual stand-level N-fixation inputs were not directly measured before the fire so annual landscape-level N-fixation inputs are not depicted in the pre-Boundary Fire map. Black spruce was concentrated along Nome Creek (northwest region of the burn) and the Chatanika River (central region of the burn) as well as immediately adjacent to tributaries of those rivers before the Boundary Fire. Areas of Mixed or Deciduous vegetation before the fire were found along steeper, higher elevation south-facing slopes. The classification of pre-fire vegetation types in the Boundary Fire resulted in an 81% overall accuracy and kappa coefficients of 81% and 67%, respectively (Table 2.1). The pre-fire Black Spruce vegetation type was slightly overestimated in the classification (95% producer's and 90% user's accuracy) (Table 2.2), while the pre-fire Deciduous vegetation type was underestimated in the classification (57% producer's and 80% user's accuracy) (Table 2.2). The pre-fire Mixed vegetation type was overestimated (70% producer's and 64% user's accuracy) (Table 2.2).

Post-fire vegetation types within the Boundary Fire were classified and annual stand-level N-fixation inputs were directly attributed to their respective vegetation type (Figure 2.4) per estimates borrowed from Chapter 1. The northwest region of the Boundary Fire was classified as Black Spruce – Moderate, which was the most closely related post-fire vegetation type to pre-fire Black Spruce, which had the second lowest annual stand-level N-fixation input (0.52 ± 0.03 kg N

ha^{-1} yr^{-1}). The lowest annual stand-level N-fixation (0.06 ± 0.003 kg N ha^{-1} yr^{-1}) occurred in the Black Spruce – High vegetation type, which dominated higher elevation ridgetops that were extremely dry. Areas of the highest annual stand-level N-fixation input (11.53 ± 0.22 kg N ha^{-1} yr^{-1}) were in the Deciduous-Moderate vegetation type that predominated the central and southern portion of the burn area along steeper, higher elevation south-facing slopes. The best classification of post-fire vegetation types in the Boundary Fire resulted in overall accuracy and kappa coefficients of 89% and 85%, respectively (Table 2.1). Producer's and user's accuracies for the Deciduous – Moderate vegetation type were 93% and 100%, respectively; thus, total Deciduous-Moderate vegetation cover was slightly underestimated across the Boundary Fire (Table 2.2). The Black Spruce – Moderate vegetation type showed even greater underestimation (50% producer's and 100% user's accuracy) than the Deciduous-Moderate type. The Black Spruce – High (100% producer's and 83% user's accuracy) and Black Spruce – Moderate to High (89% producer's and 80% user's accuracy) were both overestimated in the classification (Table 2.2).

Annual Landscape-level N-fixation Input

The Deciduous vegetation type occupied roughly 38% of the area but contributed 60% of total annual landscape-level N-fixation inputs by Siberian alder within in the Wickersham Dome Fire (Table 2.3, Figure 2.5). The Black Spruce vegetation type of the Wickersham Dome Fire made up 42% of the area but contributed only 12% of annual landscape-level N-fixation inputs by Siberian alder (Table 2.3, Figure 2.5). Estimates of pre-fire landscape-level N-fixation input for the Boundary Fire were based on Wickersham Dome Fire estimates of annual stand-level N-fixation input for Black Spruce, Mixed, and Deciduous vegetation types; however, stand area

was calculated using the pre-Boundary Fire classified map. Annual stand-level N-fixation input (as taken from the Wickersham Dome Fire) for the Black Spruce vegetation type was approximately 80% lower than the Mixed and Deciduous vegetation types (Table 2.3, Figure 2.5). The Black Spruce vegetation type accounted for nearly 74% of the area but contributed 34% of the annual landscape-level N-fixation input by Siberian alder before the Boundary Fire (Table 2.3, Figure 2.5). The Mixed and Deciduous vegetation types made up 15% and 11% of the area, respectively, but accounted for 37% and 30% of annual landscape-level N-fixation input by Siberian alder in the pre-Boundary Fire study area (Table 2.3, Figure 2.5).

After the fire, approximately 70% of the Boundary Fire study area was covered by a variant of the black spruce vegetation type (Black Spruce-Moderate, Black Spruce-Moderate to High, Black Spruce-High) while only 28% was covered by the Deciduous-Moderate vegetation type (Table 2.3, Figure 2.5). However, because the annual stand-level N-fixation inputs for the Deciduous-Moderate vegetation type were over four times greater than the three black spruce vegetation types combine (Table 2.3), approximately 84% of annual landscape-level N-fixation input within the Boundary Fire study area occurred in the Deciduous-Moderate vegetation type (Table 2.3, Figure 2.5).

Changes to Annual Landscape-level N-fixation Input

We found that 16,360 ha (42%) of the pre-fire Black Spruce vegetation type remained black spruce in the form of the Black Spruce-Moderate vegetation type (Table 2.4, Figure 2.6). Approximately 14,353 ha (36%) converted to a deciduous-dominated vegetation type (of which, 5,392 ha (14%) was Deciduous-Moderate and 8,961 ha (22%) was Black Spruce-High (a vegetation type dominated by post-fire deciduous tree seedlings)), while the remaining 9,070 ha

(22%) of pre-fire Black Spruce vegetation type converted to a post-fire mixed vegetation type (in the form of Black Spruce-Moderate to High) (Table 2.4, Figure 2.6). Of the pre-fire Mixed vegetation type, 1,601 ha (20%) remained mixed (as Black Spruce-Moderate to High), 656 ha (9%) converted to a black spruce vegetation type (as Black Spruce-Moderate), and 5,706 ha (70%) converted to a deciduous vegetation type (of which, 1494 ha (19%) was Black Spruce-High, and 4,212 ha (52%) was Deciduous-Moderate) (Table 2.4, Figure 2.6). Within the pre-fire Deciduous vegetation type 5,605 ha (91%) remained deciduous (of which, 288 ha (5%) was Black Spruce-High, and 5,317 ha (86%) was Deciduous-Moderate), 93 ha (2%) converted to a black spruce vegetation type (as Black Spruce-Moderate), and 418 ha (7%) converted to a mixed vegetation type (as Black Spruce-Moderate to High) (Table 2.4, Figure 2.6).

Due to strong differences in annual stand-level N-fixation input among pre-Boundary Fire (estimated from 44-year old Wickersham Dome Fire) and post-Boundary Fire vegetation types (Table 2.4), as well as marked conversions in area from a low N-input vegetation type to a high N-input vegetation type (Table 2.4, Figure 2.6), each pre-fire vegetation type showed a net increase in total annual landscape-level N-fixation input (+33.33, +17.14, and +56.24 t N yr^{-1} for the Deciduous, Mixed, and Black Spruce vegetation types, respectively) (Table 2.4, Figure 2.7). Most of the increase in annual landscape-level N-fixation input for each vegetation type was the result of very high differences in annual landscape-level N-fixation inputs between all pre-fire vegetation types and the post-fire Deciduous-Moderate vegetation type (+36.21, +30.03, and +57.69 t N yr^{-1} for the Deciduous, Mixed and Black spruce vegetation types, respectively) (Table 2.4, Figure 2.7). Interestingly, all net gains of Siberian alder N-input occurred in areas that either remained or converted to a deciduous vegetation type (44% of the study area), while most losses in N-input occurred in the other 56% of the study area. As such, even a slight net-positive

increase to the deciduous vegetation type following a fire may, on average, result in a substantial net-positive increase to annual landscape-level N-fixation inputs across the entire burned area. Even areas that were pre-fire deciduous and remained deciduous after the fire (i.e. Deciduous-Moderate) showed a considerably increase in annual landscape-level N-fixation input (+36.21 t N yr^{-1}) (Table 2.4, Figure 2.7). Increases of landscape-level N-fixation input along the pre-fire deciduous to post-fire deciduous pathway are due to higher nodule-level N-fixation and nodule biomass following fire, as determined in Chapter 1. The largest difference between pre- and post-fire annual landscape-level N-fixation inputs was the result of conversions from pre-fire Black Spruce to the post-fire Deciduous-Moderate (deciduous) vegetation type (+57.69 t N yr^{-1}) (Table 2.4, Figure 2.7).

The map of conversion or non-conversion pathways and their related change in annual landscape-level N-fixation input (Figure 2.8) shows that the largest area of unchanged vegetation type in this study was black spruce dominated before the Boundary Fire and remained black spruce dominated after the fire (i.e. BS → BS-M). Yet, due to differences in annual stand-level N-fixation inputs before and after the Boundary Fire, we estimated a reduction in annual landscape-level N-fixation inputs for those areas that persisted as black spruce dominated (-5.07 t N yr^{-1}) (Table 2.4, Figure 2.6). Areas of unchanged black spruce (BS → BS-M) generally occurred in areas of mesic soils that had stunted black spruce-tussock tundra on a steppe just above the Beaver River and its tributaries – north and northwest portions of the Boundary Fire (Figure 2.8). The isolated pockets of unchanged black spruce around the central portion of the Boundary Fire area were located on a similarly mesic black spruce – tussock tundra plant community located adjacent to and several meters above the Chatanika River (Figure 2.8). Most of the stand conversions from black spruce to either a mixed (BS → BS-M to H) or deciduous

(BS → D-M) vegetation type occurred along warmer, drier, and steeper southeast, south, and southwest facing slopes, which are in the middle and southern portions of the Boundary Fire area (Figure 2.8). The displacement of pre-fire black spruce in lieu of a post-fire mixed or deciduous vegetation type seems to occur predominately on well-drained, warmer soils, whereas the persistence of black spruce following fire seems to be most closely related to areas of poorly drained, colder soil types.

DISCUSSION

Fire Effects on Landscape N-input

In the pre-Boundary Fire classification, Black Spruce stands accounted for 39,783 ha of the total Boundary Fire study area (74%). Since black spruce stands of the Boundary Fire lost an average of 900 kg N ha^{-1} upon combustion of above- and belowground (soil organic layer) biomass (Boby et al. 2010), approximately 35,805 metric tons of N was combusted from the pre-fire Black Spruce stands of the Boundary Fire study area. Post-fire Siberian alder inputs in this stand type totaled 89 t N yr^{-1}; therefore, Siberian alder N-inputs would recover N-losses from burned black spruce stands after 402 years of post-fire secondary succession. Yet, of those black spruce stands that burned, 16,360 ha followed a black spruce trajectory after the fire (Black Spruce-Moderate vegetation type), which lost 14,724 t N in the fire. Since Siberian alder N-input rates are very low in the post-fire Black Spruce-Moderate vegetation type (8.51 t N yr^{-1}), it would take approximately 1,730 years of post-fire secondary succession for alder to offset N-losses in these stands, if alder N-fixation rates remain constant. Fires in the boreal forest are predicted to be larger, of higher fire severity, and occur more frequently as a result of climate

change (Wotton et al. 2010). Under such a scenario, N-losses due to volatilization would increasingly offset Siberian alder N-input; thus, additional sources of N-input would be necessary to avert long-term N pool depletions. If Siberian alder N-inputs were combined with atmospheric deposition and feathermoss N-fixation (0.3 kg N ha^{-1} yr^{-1} and 2 kg N ha^{-1} yr^{-1}, respectively) (DeLuca et al. 2002; Gundale et al. 2011), then the average amount of N recovery for the pre-fire Black Spruce area would be 198 years, while areas that remained on a black spruce trajectory after the fire (Black Spruce-Moderate) would require 320 years to recovery N losses. Given that the N-recovery times of this study exceed historic fire return intervals (Kasischke et al. 2002), and that fire effectively reduces alder populations in black spruce stands, Siberian alder N-fixation inputs alone, or combined with atmospheric deposition and bryophyte N-fixation, seem unlikely to recover N-losses in moderate severity fire.

Over half of the area within the black spruce to deciduous conversion pathway consisted of high-severity stands (Black Spruce-High) that had Siberian alder N-input rates over an order of magnitude lower than moderate-severity stands (Deciduous-Moderate), a relationship driven primarily by the negative impacts of high fire severity on alder density (Chapter 1). We applied the high severity 1400 kg N ha^{-1} volatilization rates from Boby et al. (2010) to the high severity black spruce stands and estimated a loss of roughly 12,545 t N during the fire. Since these high-severity black spruce stands recover 0.54 t N yr^{-1} from Siberian alder N-input it would require 23,231 years of post-fire succession for Siberian alder N-input to recover N losses. If we combine Siberian alder N-input with N-deposition and feathermoss N-fixation inputs (21 t N yr^{-1}), it would take 582 years to fully offset losses of N in high severity black spruce stands. Conversely, areas within the moderately burned black spruce to deciduous conversion pathway lost approximately 4,853 t N (900 kg N ha^{-1} volatilization rate) during the fire, but high Siberian

alder N-input (62 t N yr-1) after the fire would offset N losses after 78 years, and when combined with N deposition and feathermoss N-fixation (12 t N yr^{-1}), could offset N losses after 66 years. At these rates, Siberian alder N-inputs alone could offset volatized N from a moderate severity fire in black spruce stands that convert to deciduous after the fire. Siberian alder N-input could also provide the required amount of N (909 to 1070 kg N ha^{-1}) to build a mature deciduous forest (55 to 77 years old) (Van Cleve et al. 1983). However, Siberian alder N-input cannot offset losses of N in high-severity black spruce stands that convert to deciduous dominance, nor can it fully supplement the N requirements of traditional deciduous forest growth, unless density of alder increases within these stand types. Conversely, Siberian alder N-input can offset losses of N and support the N requirements of deciduous forest growth in moderately burned black spruce stands that convert to deciduous dominance.

We must emphasize that successive burn scars will spatially overlap one another over time, and such a burn scar mosaic is likely to be associated with a mosaic pattern of Siberian alder distribution and N-input across the landscape. As a result, estimates of volatized N and Δ annual landscape-level N-fixation are likely to vary with the predicted increases to fire severity and decreases of fire return intervals (Kelly et al. 2013). High-severity fire initially lowers alder density in stands that convert from black spruce to deciduous (Chapter 1), but moderate to high severity fire initially increases alder density in black spruce stands that do not convert to deciduous. The spatial pattern of fire severity within a burn scar (i.e. the amount of area within each burn severity class) will strongly influence whether landscape-level Siberian alder N-input shows a net-increase or decrease. Though patterns of Siberian alder density may vary within post-fire black spruce after a single fire, several fire cycles may cause large areas to convert from black spruce to deciduous, and the newly converted deciduous stands, which are of lower

flammability (Bonan et al. 1990; Kasischke et al. 1995) may act as fire breaks (Epting and Verbyla 2005) to protect alder populations recruiting over time within those deciduous stands and thus bring about long-term increases to Siberian alder density and Siberian alder N-input.

Where Does All the N Go?

Studies of belowground N pools (top of soil organic layer to interface with mineral soil horzion) across stand types have shown mixed results, with some showing no difference in belowground N pools between black spruce and deciduous stands (Alexander and Mack 2016), and others finding (Melvin et al. 2015) significantly more belowground N in black spruce versus deciduous stands. Regardless of belowground N differences by stand, significantly higher rates of annual net primary productivity (ANPP) and aboveground C and N (found in stemwood) in deciduous versus black spruce stands throughout post-fire succession (Melvin et al. 2015; Alexander and Mack 2016) are likely dependent on higher rates of N-mineralization (Melvin et al. 2015), higher annual stand-level N-fixation input by alder (Chapter 1), and other significant sources of N in deciduous stand types. Siberian alder's affinity for the same conditions that support productive deciduous tree growth – subxeric soils of shallow O horizon within younger burn scars (Chapter 1) – combined with low belowground N storage in these deciduous stands suggests that excess Siberian alder N-inputs may be rapidly incorporated for deciduous tree growth. Additionally, the uptake of soil N by deciduous trees may be acting to limit N saturation around alders that would otherwise experience down-regulation of N-fixation due to high soil N:P ratios (Ruess et al. 2013), such a relationship may explain Siberian alder's increasing N-fixation inputs through late-age secondary succession.

Biogeochemical processes often occur in patches of disproportionally high rates (or hot spots) across an otherwise uniform landscape (McClain et al. 2003). Though our maps of the Boundary Fire show vegetation types that cover an area as large as 100 km^2, actual N-inputs within each vegetation type reflect patterns of alder density, which are quite patchy within a stand (personal observation by Brian Houseman). Yet alder patches act as hot spots of N-input

that will grow over successional age and can persist for decades or centuries (Mitchell and Ruess 2009). Predictions of increased fire severity because of climate change (Calef et al. 2015) are associated with a predicted transition from black spruce to deciduous trajectories (Johnstone et al. 2010) and our results suggest an increasingly large Siberian alder N-input in deciduous stand alder patches that will expand over successional age while fueling post-fire deciduous forest growth.

Conversions vs Differentiation of Stand Subtype

Some of the reductions in Siberian alder N-input as a result of conversions are probably confounded by the lumping of two black spruce subtypes into a single vegetation type before the fire and by the separation of black spruce subtypes into three different post-fire vegetation types. Within the upland boreal forest around Fairbanks the black spruce community type is separated into a wet acidic subtype defined by species composition, and a dry acidic subtype that lacks the wet acidic diagnostic species (Hollingsworth et al. 2006). The same environmental characteristic that differentiates black spruce subtypes - soil moisture - has a strong negative correlation with alder density across all stand types from early to intermediate age (Chapter 1) and a negative effect on fire severity (Dyrness and Norum 1983; Kasischke and Johnstone 2005). There is a negative indirect effect of fire severity on alder density within black spruce stands (Chapter 1). The pre-fire black spruce vegetation type used in our analysis does not differentiate between wet acidic and dry acidic, but our three post-fire black spruce vegetation types differ by fire severity and somewhat by site moisture (Appendix 2.A). Thus, a complex interaction among site moisture, Siberian alder density, and fire severity suggests that Siberian alder N-input may not have been uniform across the pre-fire Black Spruce vegetation type, rather N-inputs were highest

in drier soils were alder density was likely highest before the fire. We hypothesize that pre-fire Black Spruce alder density was likely highest in areas that later became post-fire Black Spruce-Moderate to High (moderate soil moisture), and lowest in areas that became Black Spruce-Moderate (high soil moisture) or Black Spruce-High (lower soil moisture but very high fire severity). Taken together, we likely overestimate reductions in Siberian alder N-input along the Black Spruce to the Black Spruce-High conversion pathway but underestimate reductions in the Black Spruce to Black Spruce-Moderate non-conversion pathway.

Classification Accuracy and Scaling Issues

In the pre-Boundary Fire classification, the Black Spruce and Mixed vegetation types were overestimated and the Deciduous vegetation type was underestimated. Mixed stands generally share similar elements of species composition with black spruce and deciduous stands across the boreal forest while the latter two stand types are quite dissimilar in species composition (Bergeron et al. 2014). The missing pixels of Deciduous vegetation type were likely to have been incorrectly classified as Mixed vegetation, while the pixels that were incorrectly placed into the Black Spruce vegetation type were likely of a Mixed vegetation type. In the post-Boundary Fire classification, the Deciduous-Moderate and Black Spruce-Moderate vegetation types were underestimated. Most of the missing pixels of Deciduous-Moderate were likely classified as Black Spruce-High because of similarities in dominant plant species cover (Appendix 2.A) that equate to similarities in Landsat spectral characteristics between these two vegetation types (Epting and Verbyla 2005). Most of the missing area of Black Spruce-Moderate was likely misclassified as Black Spruce-Moderate to High given strong similarities in

the amount of black spruce, *Vaccinium* sp., and *Rhododendron* sp. cover between these two vegetation types (Appendix 2.A).

A more accurate classification of pre-Boundary Fire vegetation types would include less black spruce stand cover and more deciduous stand cover than shown in our results. An improved post-fire map would also include more deciduous stand and black spruce stand cover and less of the mixed stand (Black Spruce-Moderate to High) and high-severity black spruce (Black Spruce-High) stand cover. If correcting the inaccuracies of our map were to, on balance, result in a more conservative scenario of stand conversion from pre- to post-fire (i.e. a greater area of black spruce stand remaining black spruce after the fire, and more deciduous stand area remaining deciduous after fire), then the absolute values and spatial pattern of annual landscape-level N-fixation input would change. However, because the relative differences between pre- and post-fire annual landscape-level N-fixation input along each conversion or non-conversion pathway are a function of differences in annual stand-level N-fixation input, we would not expect the relationship between pre- and post-fire annual landscape-level N-inputs to change within each pathway. As such, fire can have a positive effect on annual landscape-level N-input that is independent of conversions from black spruce to deciduous stand type.

Substituting Wickersham Dome Fire for Pre-fire Boundary Fire

Fire history records indicate that pre-Boundary Fire stands were over 60-years old (late age successional) prior to burning (Alaska Fire Service 2016). The pre-Boundary Fire stand-level N-fixation inputs used in this study were substituted with estimates from 44-year old (intermediate age) Wickersham Dome Fire stands. Successional changes in alder growth traits from intermediate to late-age succession would likely alter our estimates of pre-Boundary Fire

annual stand-level N-fixation input, thus altering our Δ annual landscape-level N-fixation input results. Siberian alder density is known to increase from early to intermediate succession in all stand types (deciduous, mixed, and black spruce) (Chapter 1) and in mixed stands from early to late succession (Mitchell and Ruess 2009), resulting in higher N-inputs. Alder density, nodule biomass, and nodule-level N-fixation were all lower across all stand types in early- and intermediate-age burn scars in wet organic soil, deep organic soil, and older burn scars, respectively (Chapter 1). Given strong similarities in the drivers of alder growth traits (organic soil moisture, O horizon depth, and post-fire age) between the upland mixed stands of Mitchell and Ruess (2009) and the upland deciduous stands of Chapter 1, Siberian alder N-input was likely higher in the actual pre-Boundary Fire deciduous stands compared to the values that we used; thus, the reductions in landscape-level N-input that we show are likely greater than we show, and increases in N-input are likely smaller than we show. The drivers of alder growth traits also suggest that, from intermediate to late succession, deciduous stands are likely to show relatively higher increases in density and lower decreases in nodule-level N-fixation than the wet and deep organic soils of black spruce stands. Changes to alder growth traits from intermediate to late succession may reduce the absolute values of Δ annual landscape-level N-fixation input along pathways that show increased N-input (e.g. Black Spruce to Deciduous-Moderate) in our study, and decrease Δ annual landscape-level N-fixation input along pathways that show decreased N-input (e.g. Black Spruce to Black Spruce-High). Differences between intermediate and late-age succession alder growth may also increase the relative difference in N-input between pre-Boundary Fire black spruce and deciduous stands; therefore fire-induced stand conversions from black spruce to deciduous dominance are very likely associated with the drastically altered Siberian alder N-inputs shown in our results.

Conclusions

Our results highlight the direct effect of fire on an important ecosystem process at the landscape scale, as well as the indirect effects of fire on highly N-reliant ecosystem processes. We observed a net-increase of Siberian alder N-input after fire across a portion of the upland boreal forest, especially within stands that convert from black spruce to deciduous dominance. However, increases in Siberian alder N-input are spatially restricted and counter losses of Siberian alder N-input in other areas of a burn scar resulting from fire-driven declines in alder density. While Siberian alder N-inputs would offset N volatilization losses within moderate severity fires that have been typical of the historic fire regime, they are unlikely to provide a short-term offset of N-losses in high severity black spruce stands where Siberian alder populations are destroyed by fire. In a landscape-level study of fire severity and post-fire secondary succession in interior Alaska, Epting and Verbyla (2005) observed higher fire severity in needle-leaf forest compared to broadleaf forest, and increasing fire severity from open needle-leaf to closed needle-leaf forest. They also found that needle-leaf (or black spruce) stand self-replacement was largely associated with low to moderate fire severity and that stand conversion was associated with high fire severity. Considering the trend of increased fire size and severity, as well as shorter fire return intervals in the boreal forest combined with high amounts of N volatilization and low amounts of Siberian alder N input in black spruce stands after high severity fire, N pools could be depleted from black spruce stands and augmented in established or newly-created deciduous stands. Such a spatial redistribution of N within the boreal forest might also be associated with landscape-level changes to the pattern and intensity of highly N-

reliant ecosystem processes. Understanding patterns and mechanisms for alder spread following fire is a critical need in assessing long-term impacts of fire on ecosystem N balance.

FIGURES

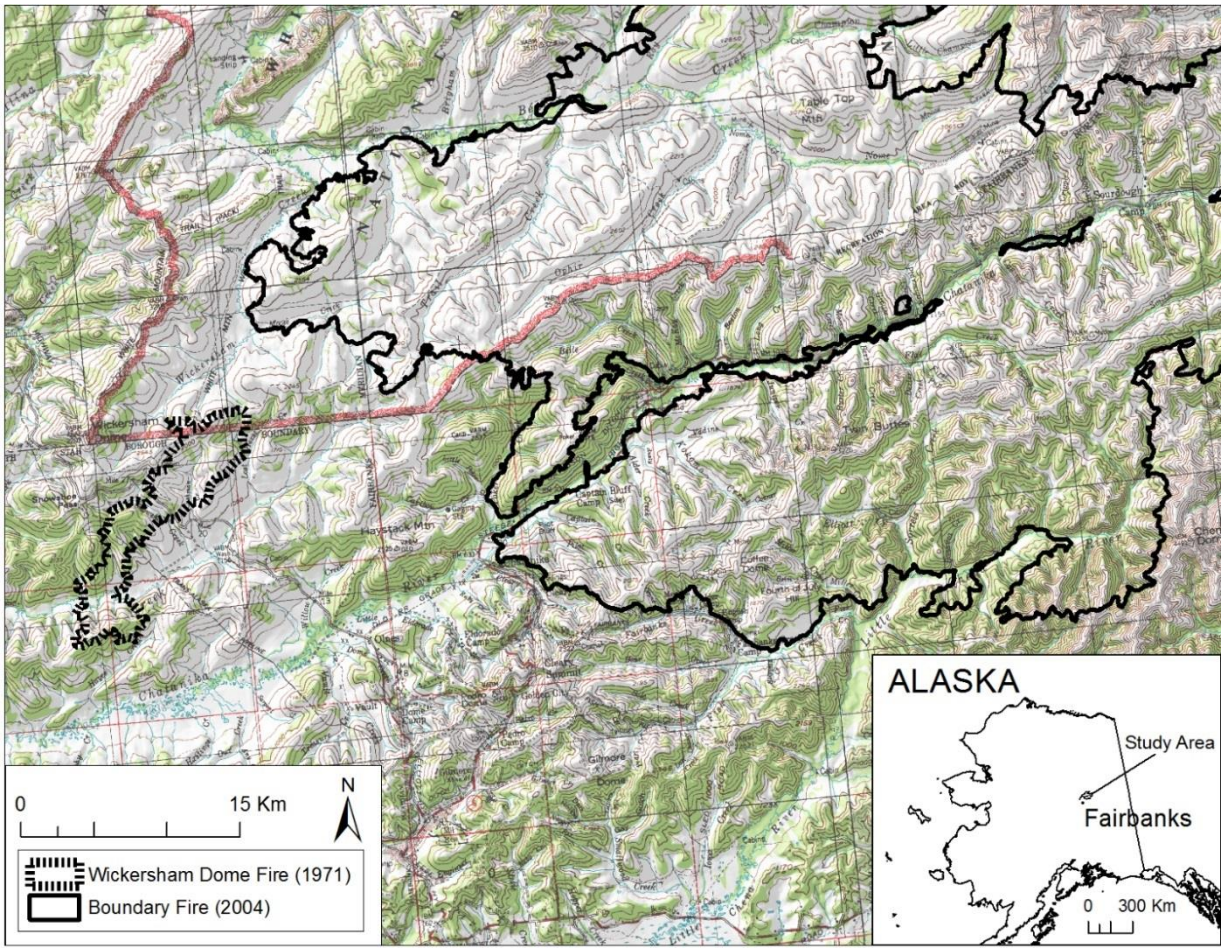

Figure 2.1. The Boundary Fire and the Wickersham Dome Fire, located approximately 35 km north of Fairbanks, Alaska.

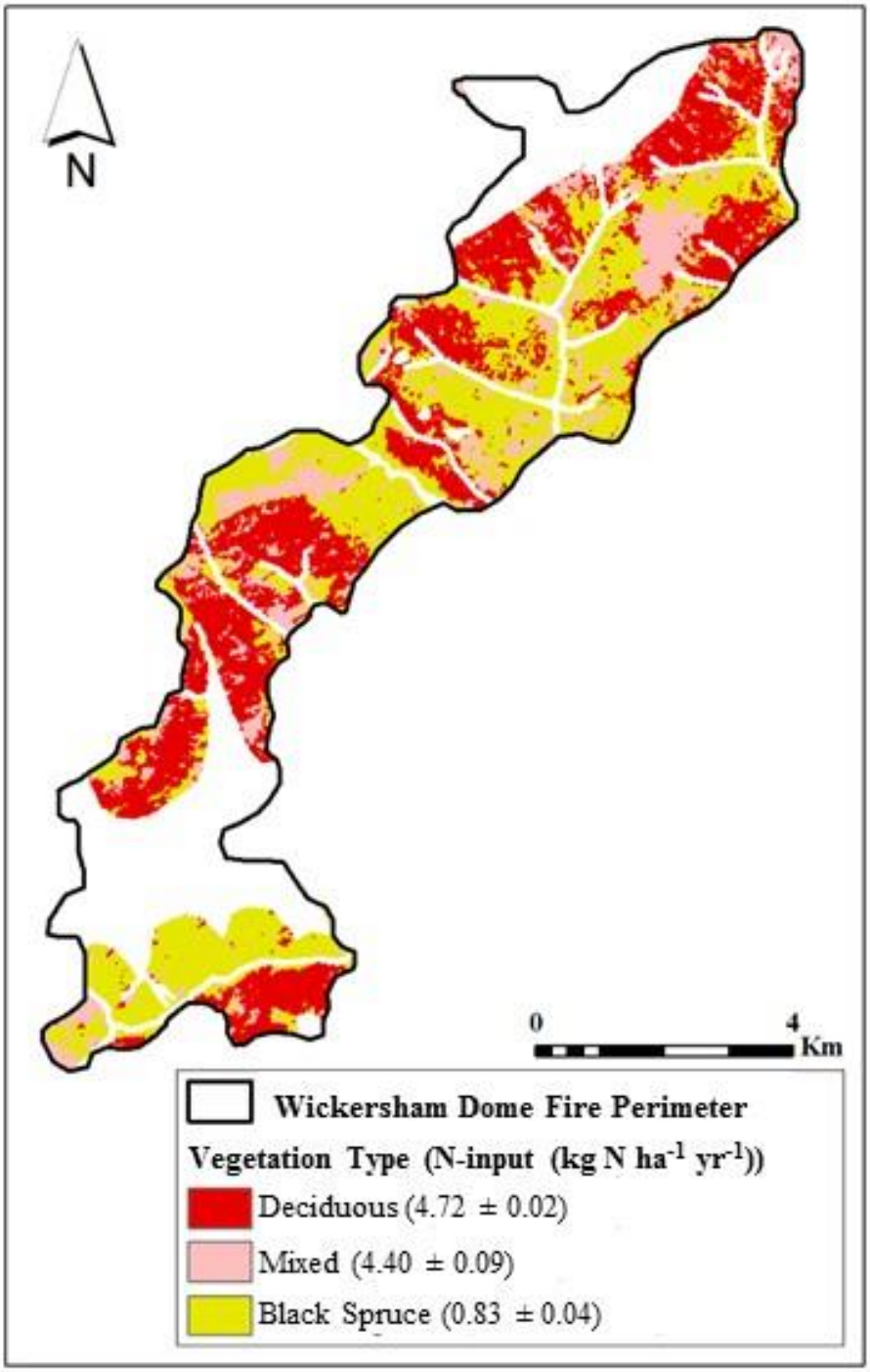

Figure 2.2. Classification of post-fire vegetation types and their current annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}) in the Wickersham Dome Fire. The classification area is limited to the same topographic and ecosystem constraints (elevation, slope, aspect, and non-riparian) sampled by the 2014 PCQ sites and therefore does fill the entire Wickersham Dome Fire area.

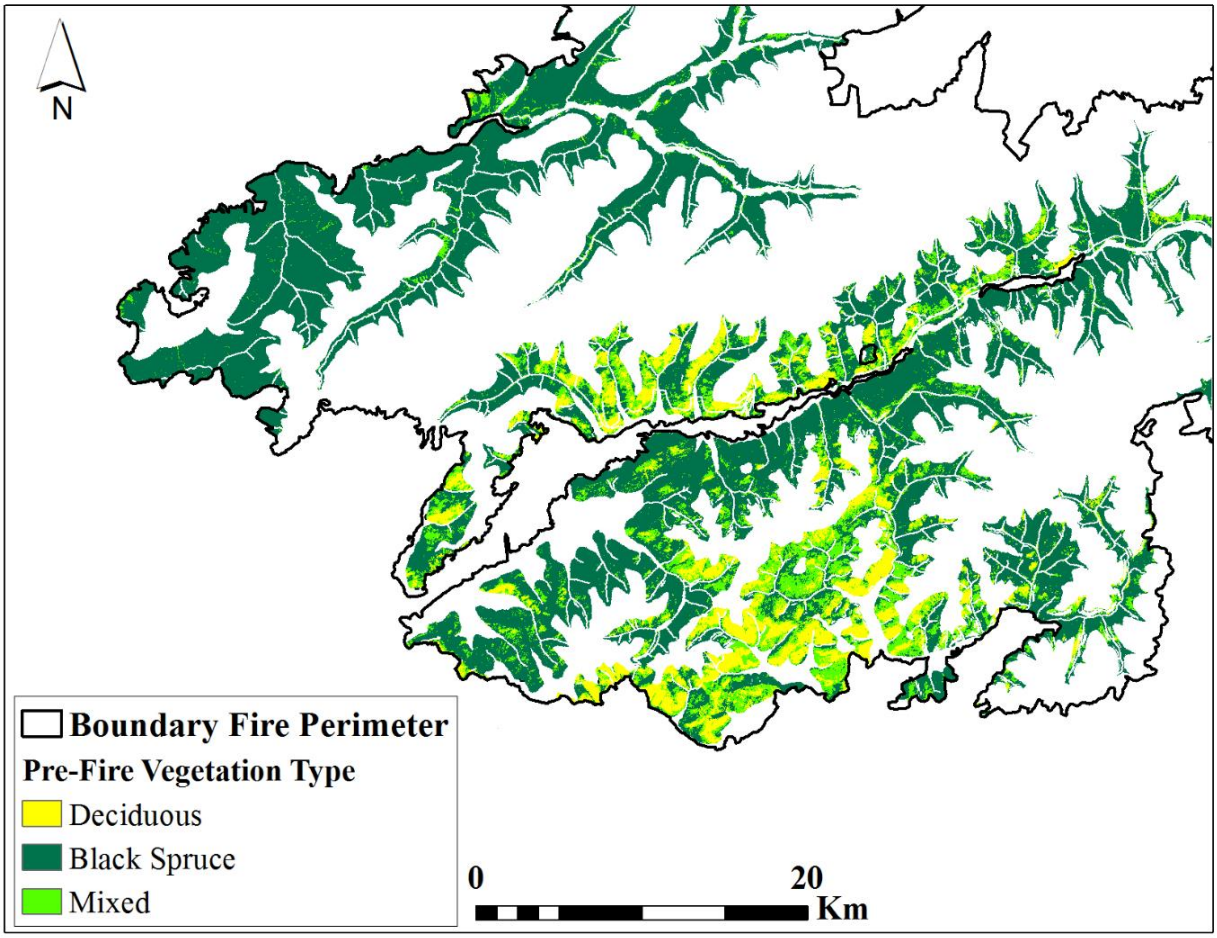

Figure 2.3. Classification of pre-fire vegetation types in the Boundary Fire using Landsat 7 ETM+ satellite imagery. The classification area is limited to the same topographic and ecosystem constraints (elevation, slope, aspect, non-riparian) sampled by the 2014 PCQ sites and therefore does not cover the entire Boundary Fire area.

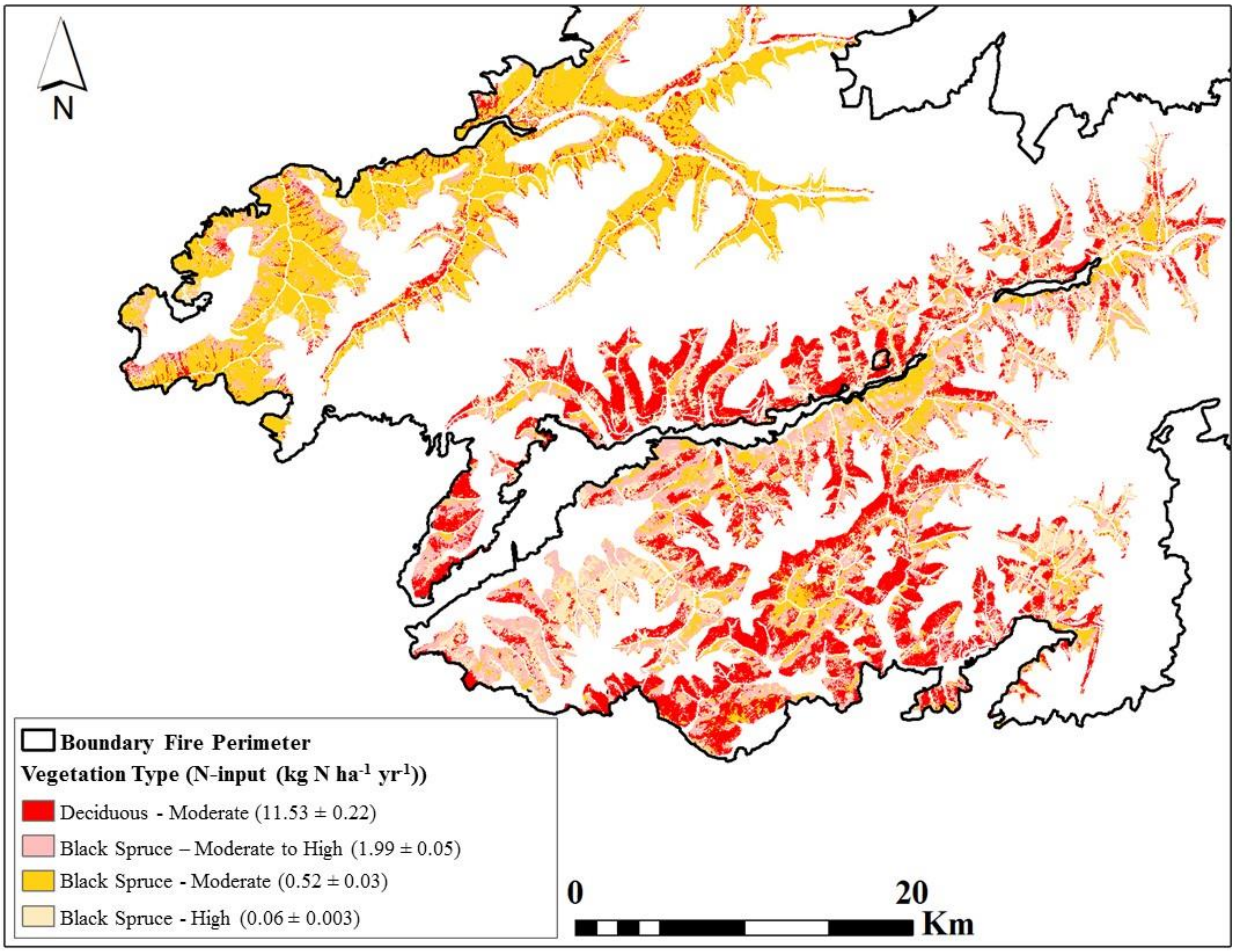

Figure 2.4. Classification of post-fire vegetation types and their annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}) in the Boundary Fire. The classification area is limited to the same topographic and ecosystem constraints (elevation, slope, aspect, and non-riparian) sampled by the 2014 PCQ sites and therefore does fill the entire Boundary Fire area.

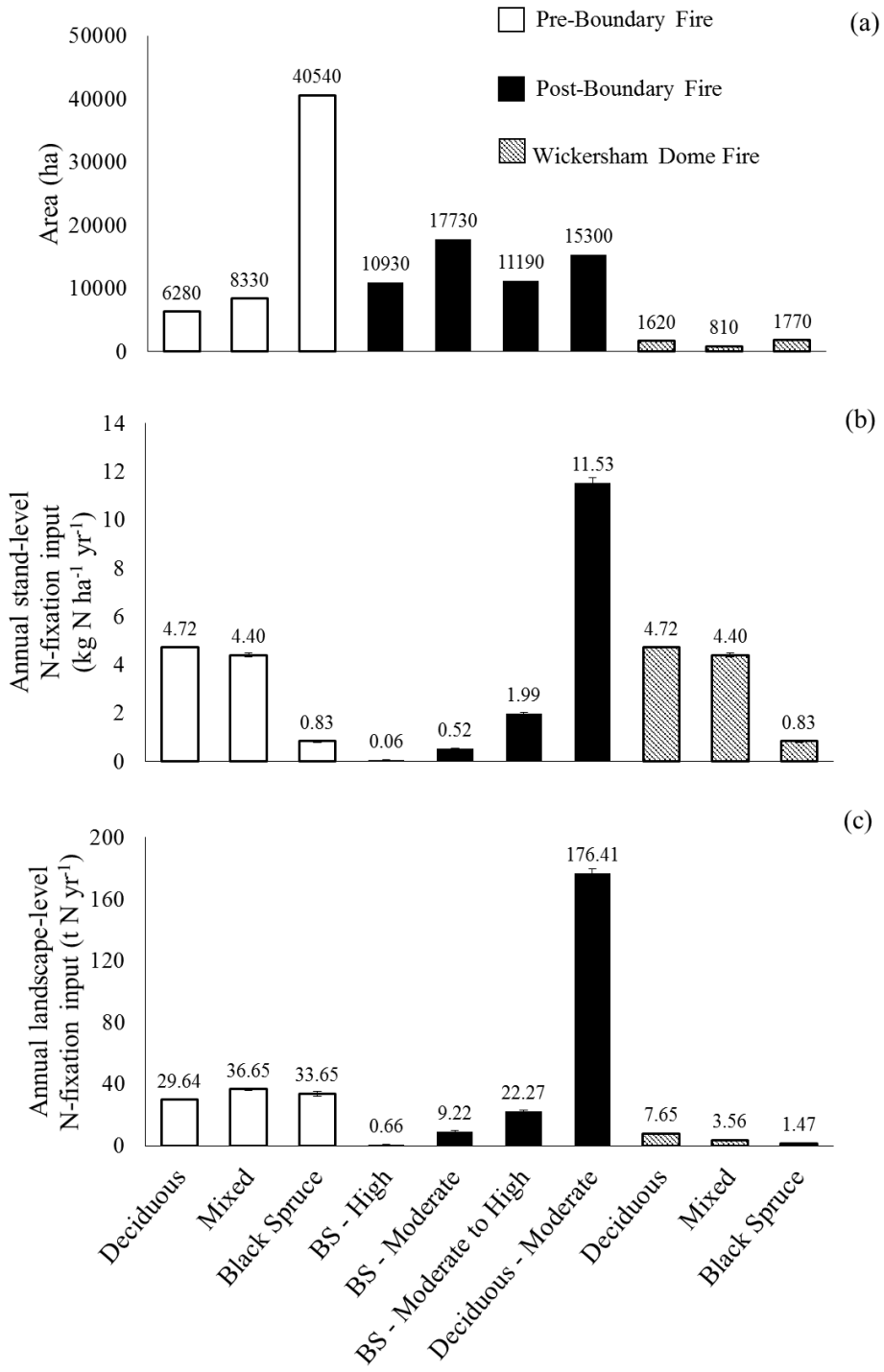

Figure 2.5. Area (ha) (a), annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}) (b), and annual landscape-level N-fixation input (t N yr^{-1}) (c) for pre- and post-fire vegetation types in the Boundary Fire, as well as post-fire vegetation types in the Wickersham Dome Fire. Pre-fire stand-level N-fixation input within the Boundary Fire is based on estimates of annual stand-level N-Fixation input for similar stands within the Wickersham Dome Fire and the vegetation type area within the Boundary Fire.

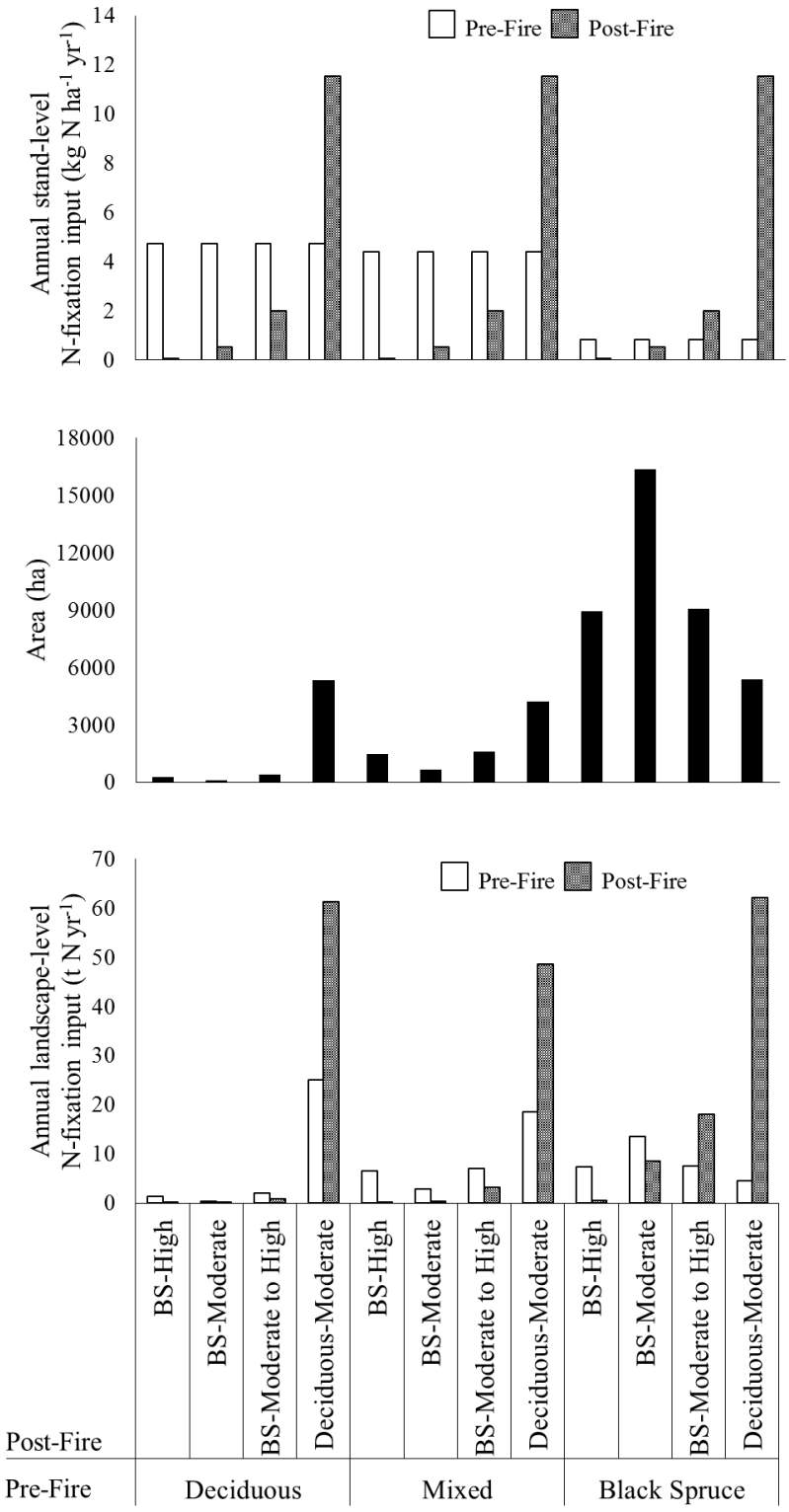

Figure 2.6. Annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}), area (ha), and annual landscape-level N-fixation input (t N yr^{-1}) in each pre- to post-fire vegetation type pathway in the Boundary Fire.

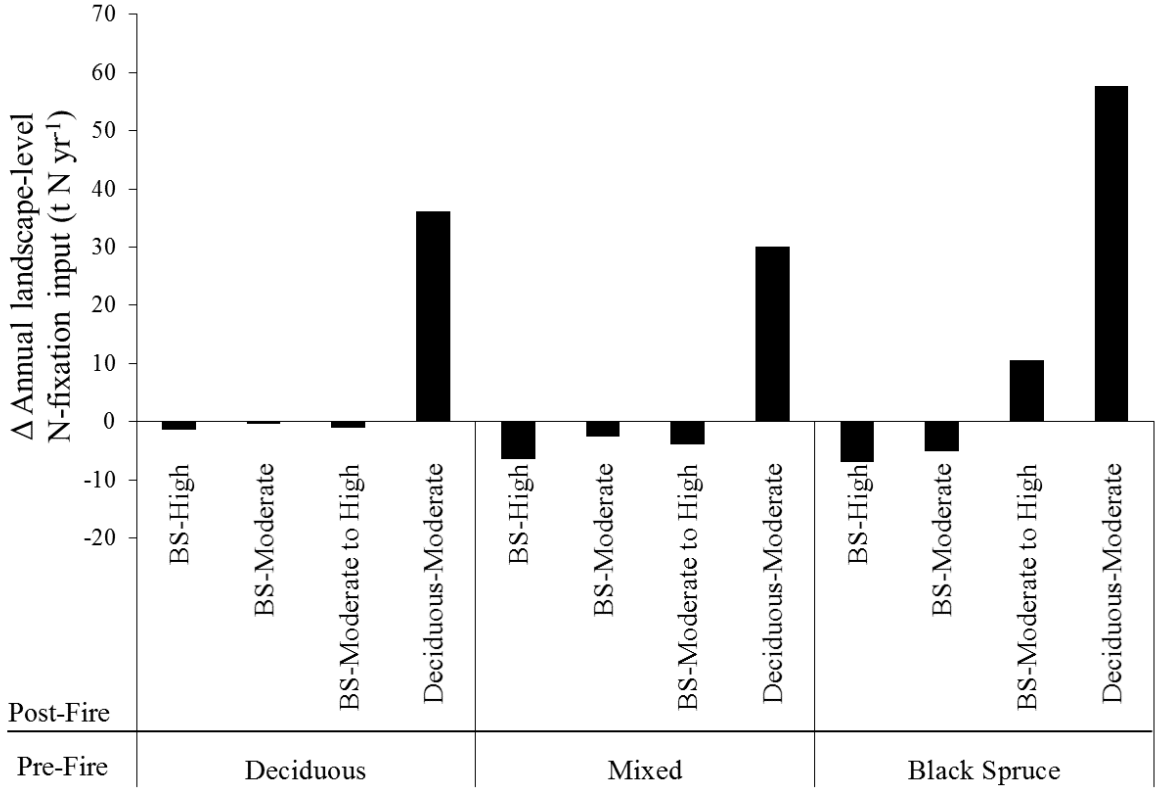

Figure 2.7. Estimated difference between pre- and post-fire annual landscape-level N-fixation input (t N yr^{-1}) in the Boundary Fire. Pre-Boundary Fire annual landscape-level N-fixation input was determined by multiplying the Wickersham Dome Fire estimates of annual stand-level N-fixation input (kg N ha-1 yr-1) for deciduous, black spruce, and mixed vegetation types by the area (ha) of those vegetation types in the Boundary Fire.

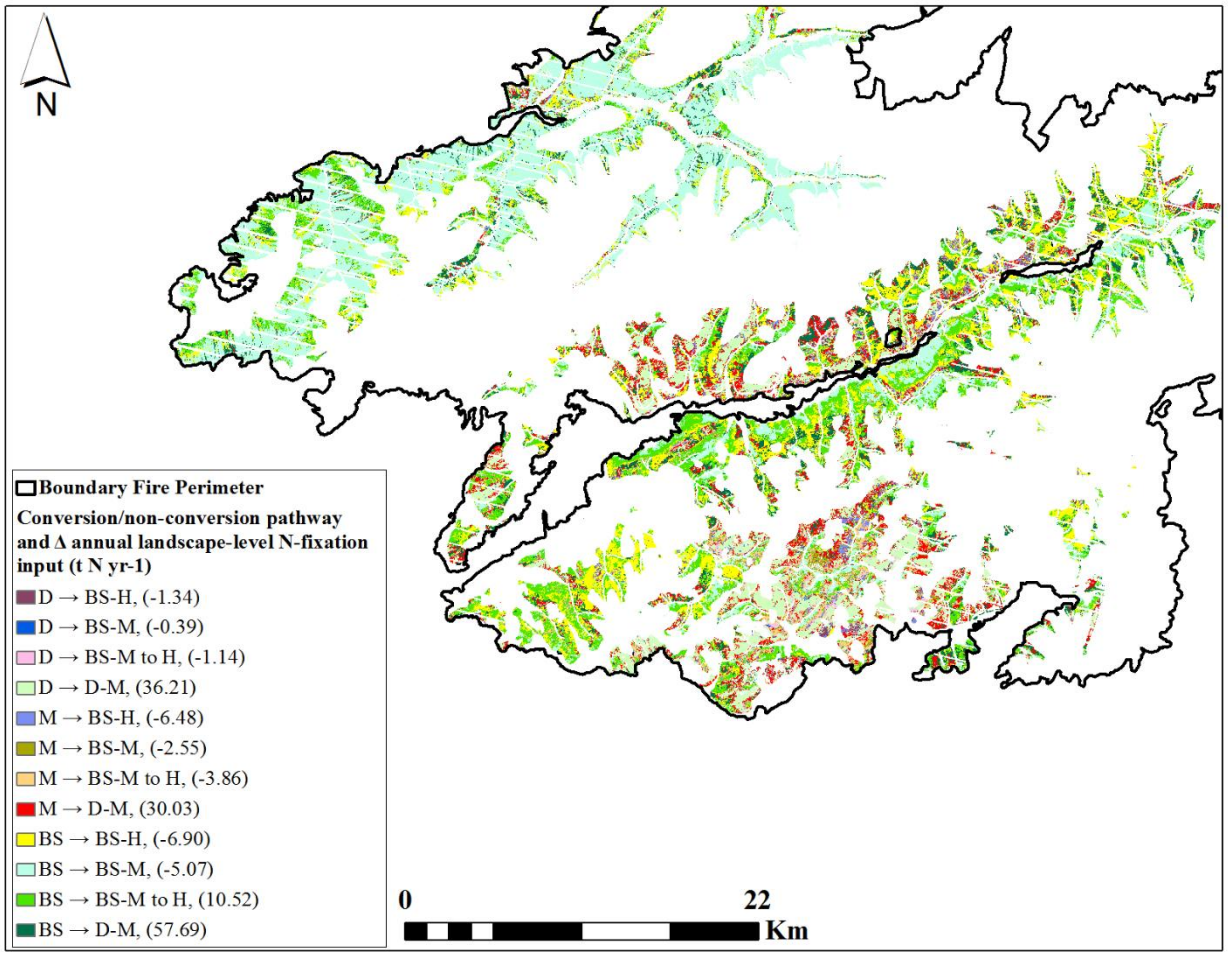

Figure 2.8. The difference between pre- and post-fire annual landscape-level N-fixation input (Δ t N yr^{-1}) in the Boundary Fire. The classification area is limited to the same topographic and ecosystem constraints (elevation, slope, aspect, and non-riparian) sampled by the 2014 PCQ sites and therefore does fill the entire Boundary Fire area. Estimates of pre-fire annual landscape-level N-fixation input were based on the stand-level N-fixation input (kg N ha-1 yr-1) for related vegetation types in the Wickersham Dome Fire.

TABLES

Table 2.1. Satellite imagery and bands used to classify pre- and post-fire vegetation types in the Boundary Fire, post-fire vegetation types in the Wickersham Dome Fire, overall accuracy (%) and kappa statistic for each image classification. Images used to classify vegetation types for each burn scar are in bold print.

Satellite	Image Date(s)	Composite Bands	Overall Accuracy (%)	Kappa statistic
Boundary Fire				
Pre-fire				
Landsat 7 ETM+	**May 27, 2002**	**3, 4, & 5**	**80.6**	**0.673**
Post-fire				
Landsat 8 OLI	May 11, 2014	4, 5, & 6	64.9	0.496
	June 15, 2015	4, 5, & 6	75.7	0.654
	May 11, 2014 and June 15, 2015	**4, 5, & 6 and 4, 5, & 6**	**89.2**	**0.847**
Wickersham Dome Fire				
Post-fire				
Landsat 8 OLI	May 11, 2014	4, 5, & 6	62.5	0.429
	June 15, 2015	**4, 5, & 6**	**75.0**	**0.626**
	May 11, 2014 and June 15, 2015	4, 5, & 6 and 4, 5, & 6	68.8	0.527

Table 2.2. Producer's and user's accuracy (%) for classified vegetation types of the Boundary Fire and Wickersham Dome Fire. Post-fire classifications were created with Landsat 8 OLI imagery, whereas pre-Boundary Fire classifications were created with Landsat 7 ETM+ imagery.

Vegetation Type	Producer's Accuracy (%)	User's Accuracy (%)
Boundary Fire		
Pre-fire		
Black Spruce	94.7	90.0
Mixed	70.0	63.6
Deciduous	57.1	80.0
Post-Fire		
Deciduous-Moderate	92.9	100.0
Black Spruce-Moderate	50.0	100.0
Black Spruce-High	100.0	83.3
Black Spruce-Moderate to High	88.9	80.0
Wickersham Dome Fire		
Post-fire		
Black Spruce	66.7	80.0
Mixed	60.0	60.0
Deciduous	100.0	83.3

Table 2.3. Annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}), stand area (ha), and landscape-level N-input (t N yr^{-1}) statistics for each vegetation type of the Boundary Fire (pre- and post-fire) and Wickersham Dome Fire (post-fire). All percentages were calculated within pre- or post-fire designation for each burn scar (e.g. all vegetation types within the pre-Boundary Fire designation).

Vegetation Type	Annual stand-level N-fixation input (kg N ha^{-1} yr^{-1})€	Stand Area (ha)*	Stand Area (%)	Annual landscape-level N-fixation input (t N yr^{-1})†	Annual landscape-level N-fixation input (%)
Boundary Fire					
Pre-fire					
Black Spruce	0.83 ± 0.04	40533	73.5	33.65 ± 1.62	33.7
Mixed	4.40 ± 0.09	8324	15.1	36.65 ± 0.75	36.7
Deciduous	4.72 ± 0.02	6270	11.4	29.64 ± 0.13	29.7
Post-fire					
Deciduous-Moderate	11.53 ± 0.22	15300	27.7	176.41 ± 3.36	84.6
Black Spruce-Moderate	0.52 ± 0.03	17730	32.1	9.22 ± 0.53	4.4
Black Spruce-High	0.06 ± 0.003	10930	19.8	0.66 ± 0.03	0.3
Black Spruce-Moderate to High	1.99 ± 0.05	11190	20.3	22.27 ± 0.56	10.7
Wickersham Dome Fire					
Black Spruce	0.83 ± 0.04	1770	42.1	1.47 ± 0.07	11.6
Mixed	4.40 ± 0.09	810	19.3	3.56 ± 0.07	28.1
Deciduous	4.72 ± 0.02	1620	38.6	7.65 ± 0.03	60.3

€ Annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}) rates for the pre-Boundary Fire vegetation types were not measured directly but instead taken from the 44-year old Wickersham Dome Fire estimates.

* Stand area values were measured directly for all vegetation types, including pre-fire. Area was not calculated from the entire area of the burn, rather from the area of the burn which fulfills the topographic and ecosystem constraints that define the study area (depicted by vegetation type in Figure 2.2, Figure 2.3, and Figure 2.4).

† Annual landscape-level N-fixation input (t N yr-1) is the product of annual stand-level N-fixation input and stand area.

Table 2.4. Stand area (ha), pre- and post-fire annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}), pre- and post-fire annual landscape-level N-fixation input (t N yr^{-1}), and the difference between pre- and post-fire annual landscape-level N-fixation input (t N yr^{-1}) for the Boundary Fire. BS = Black Spruce.

Pre- and Post-Fire Vegetation Type	Stand Area (ha)*	Pre-fire annual stand-level N-fixation input (kg N ha^{-1} yr^{-1})€	Pre-fire annual landscape-level N-fixation input (t N yr^{-1}) †	Post-fire annual stand-level N-fixation input (kg N ha^{-1} yr^{-1})	Post-fire annual landscape-level N-fixation input (t N yr^{-1})§	Δ Annual landscape-level N-fixation input (t N yr^{-1})
Deciduous	6116					33.33
BS-High	288	4.72 ± 0.02	1.36	0.06 ± 0.003	0.02	-1.34
BS-Moderate	93	4.72 ± 0.02	0.44	0.52 ± 0.3	0.05	-0.39
BS-Moderate to High	418	4.72 ± 0.02	1.97	1.99 ± 0.05	0.83	-1.14
Deciduous-Moderate	5317	4.72 ± 0.02	25.1	11.53 ± 0.22	61.3	36.21
Mixed	7963					17.14
BS-High	1494	4.40 ± 0.09	6.57	0.06 ± 0.003	0.09	-6.48
BS-Moderate	656	4.40 ± 0.09	2.89	0.52 ± 0.3	0.34	-2.55
BS-Moderate to High	1601	4.40 ± 0.09	7.05	1.99 ± 0.05	3.19	-3.86
Deciduous-Moderate	4212	4.40 ± 0.09	18.53	11.53 ± 0.22	48.56	30.03
Black Spruce	39783					56.24
BS-High	8961	0.83 ± 0.04	7.44	0.06 ± 0.003	0.54	-6.90
BS-Moderate	16360	0.83 ± 0.04	13.58	0.52 ± 0.3	8.51	-5.07
BS-Moderate to High	9070	0.83 ± 0.04	7.53	1.99 ± 0.05	18.05	10.52
Deciduous-Moderate	5392	0.83 ± 0.04	4.47	11.53 ± 0.22	62.16	57.69
Boundary Fire Study Area	53862		96.93		203.64	106.70

* Stand area values were measured directly for all vegetation types, including pre-fire. Area was not calculated from the entire area of the burn, rather from the area of the burn which fulfills the topographic and ecosystem constraints that define the study area (depicted in Figure 2.3 and Figure 2.4).

€ Pre-fire annual stand-level N-fixation input (kg N ha^{-1} yr^{-1}) rates were not measured directly but instead taken from the 44-year old Wickersham Dome Fire estimates.

Table 2.4 cont.

† Pre-fire annual landscape-level N-fixation input (t N yr^{-1}) is the product of stand area and pre-fire annual stand-level N-fixation input.

§ Post-fire annual landscape-level N-fixation input is the product of stand area and post-fire annual stand-level N-fixation input.

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APPENDIX

Appendix 2.A. Vegetation types sampled in the Wickersham Dome Fire and the Boundary Fire. Environmental characteristic descriptions are relative within each burn scar and not across burn scars. Fire severity is listed by class with dNBR values in parentheses; different letters indicate significant differences at $P < 0.05$. AVC name reflects the Alaska Vegetation Classification (Viereck et al. 1992).

Vegetation Type (Burn Scar)	**Indicator Species (by descending indicator value)**	**Tree Height and Cover**	**Environmental Characteristics**	**AVC Class (by descending proportion of plots in this type)**
Black Spruce (WDF)	Mosses, *Rhododendron groenlandicum, Vaccinium vitis-idaea, Picea mariana* (seedling), *Betula glandulosa, Sphagnum* sp., *Equisetum* sp., *Eriophorum* sp., *Rubus chamaemorus, Polygonum alpinum, Rhododendron palustre* ssp. *decumbens*	*Picea mariana* (8 m, 18%), *Betula neoalaskana* (7 m, 3%), *Larix laricina* (3 m, < 1%), *Populus tremuloides* (1 m, < 1%).	Lowest elevation and solar radiation; deepest organic soils (especially Oe); low mineral soil bulk density; high mineral soil % N, % C, C:N ratio, and N:P ratio	Black spruce woodland (I.A.3.d); open black spruce forest (I.A.2.f.). Similar to wet acidic black spruce muskeg described in Hollingsworth et al. 2006.

Appendix 2.A cont.

Deciduous (WDF)	Litter, *Betula neoalaskana* (tree), *Populus tremuloides* (tree), dead and down trees, *Populus tremuloides* (seedling), *Rosa acicularis*, *Geocaulon lividum*, *Picea glauca* (tree)	*Betula neoalaskana* (14 m, 40%), *Populus tremuloides* (13 m, 20%), *Picea mariana* (10 m, 10%), *Picea glauca* (17 m, 1 %)	Moderate elevation; highest solar radiation; shallow organic soils (especially Oe); high mineral soil bulk density; low mineral soil % N, % C, C:N ratio, and N:P ratio	Closed broadleaf forest (I.B.1 (d,e,f)); open broadleaf forest (I.B.2 (a,b)); closed mixed forest (I.C.1 (a,c,d)); open mixed forest (I.C.2 (a,b))
Mixed (WDF)	Lichens, *Picea mariana* (tree), *Vaccinium uliginosum*, *Salix* sp., *Cornus canadensis*, *Empetrum nigrum*	*Picea mariana* (9 m, 25%), *Betula neoalaskana* (10.5 m, 15%), *Populus tremuloides* (11 m, 4%)	Highest elevation; moderate solar radiation; shallow organic soil; low mineral soil C:N ratio	Open black spruce-paper birch forest (I.C.2.a); black spruce-paper birch woodland (I.C.3.a)

Appendix 2.A cont.

Deciduous-moderate (BF)	*Betula neoalaskana* (tree), *Betula neoalaskana* (seedling), litter, *Calamagrostis* sp., dead and down trees, *Populus tremuloides* (seedling), *Chamerion angustifolium*, *Rubus idaeus*, *Cornus canadensis*, *Populus tremuloides* (tree), *Rosa acicularis*, *Lycopodium* sp.	*Betula neoalaskana* (10 m, 12%), *Populus tremuloides* (9 m, 5%), *Picea mariana* (7.5 m, 1.5%), *Picea glauca* (16 m, < 1%).	Highest solar radiation; shallow, warm, and dry organic soils; low mineral soil % P; moderate fire severity (354 ± 30 a)	Deciduous woodland (birch, aspen, birch-aspen; I.B.3); deciduous open forest (birch, aspen, birch-aspen; I.B.2)

Appendix 2.A cont.

Black Spruce-moderate (BF)	*Sphagnum* sp., *Rubus chamaemorus*, *Picea mariana* (tree), Lichen, *Rhododendron palustre* ssp. *decumbens*, *Eriophorum* sp., *Vaccinium vitis-idaea*, *Picea mariana* (seedling), *Vaccinium oxycoccos*, Moss, *Betula nana*, *Empetrum nigrum*, *Andromeda polifolia*, *Polygonum alpinum*, *Petasites frigidus*	*Picea mariana* (5 m, 7.5%), *Betula neoalaskana* (6.5 m, < 1%).	Low solar radiation; deep, cold, and wet organic soils; moderate fire severity (350 ± 35 a)	Open low scrub (II.C.2); open black spruce forest (I.A.2.f); black spruce woodland (I.A.3.d)

Appendix 2.A cont.

Black Spruce-high (BF)	*Salix* sp. and *Carex* sp.	*Populus tremuloides* (4.5 m, 1%), *Picea mariana* (6.5 m, < 1%), and *Betula neoalaskana* (7 m, < 1 %)	High solar radiation, (second only to Deciduous-moderate); high fire severity (664 ± 28 c)	Open low scrub (II.C.2); aspen woodland (aspen) (I.B.3)

Appendix 2.A cont.

Black Spruce-moderate-to-high (BF)	*Vaccinium uliginosum*, *Rhododendron groenlandicum*, *Betula glandulosa*, *Betula* sp. (hybrid shrub), *Arctogrostis latifolia*	*Picea mariana* (5.5 m, 1.5%), *Betula neoalaskana* (7.5 m, 1.5%), *Populus tremuloides* (7 m, 1.5%), *Picea glauca* (10.5 m, < 1%), *Larix laricina* (4.5 m, < 1%)	Low solar radiation; deep organic soils; high mineral soil % P; moderate to high fire severity (499 ± 28 d)	Open low scrub (II.C.2); black spruce woodland (I.A.3.d); open birch-aspen forest (I.B.2)

CONCLUSIONS

This study shows that fire in the upland boreal forest of interior Alaska reduces Siberian alder density in pre-fire black spruce stands and therefore Siberian alder N-input, and high fire severity leads to the largest post-fire decreases in Siberian alder N-input. Landscape-level changes to Siberian alder N-input are dependent on spatial patterns of pre-fire stand type and fire severity, as well as the amount of area that converts from one pre-fire stand type to a distinctly different post-fire stand type following fire. The robust distance-based density estimates of Siberian alder in this study have shown that N-fixation inputs by Siberian alder dramatically increase total N pools immediately after fire and into intermediate-age succession, and therefore significantly affect N-reliant ecosystem processes in the boreal forest.

Patch-scale calculations of this study indicate that nodule-level N fixation rates of Siberian alder can be comparable to those measured in thin-leaf alder (*A. tenufolia*) growing along boreal forest floodplains (Uliassi and Ruess 2002, Anderson et al. 2004, Ruess et al. 2009, Ruess et al. 2013); however, the generally low density of Siberian alder within various stand types limits actual stand-level N-fixation input. Because a greater area of the interior Alaskan boreal forest likely favors Siberian alder patches over thin-leaf alder patches, the landscape-level N-inputs of Siberian alder are likely higher than thin-leaf alder. Siberian alder stand-level N-fixation inputs also seem to be higher than estimates of bryophyte N-fixation inputs for most stand types and ages (except intermediate- to late-successional black spruce stands where alder density is very low and bryophyte cover is often high). Thus, Siberian alder may be the most important post-fire N-fixer in the interior Alaskan boreal forest and therefore a significant factor in N-loss recovery after fire.

Fire severity and nodule biomass seem to share a complex relationship in black spruce stands, wherein both low and high fire severity lead to lower nodule biomass than moderate-to-high fire severity – resulting in higher plant-level N-fixation inputs in stands that experienced moderate-to-high fire severity compared to stands of low or high fire severity. Black spruce stands of high fire severity have even lower plant-level N-fixation input than both moderate and moderate-to-high severity stands due to drastic reductions in alder density. These results highlight a potential threshold in fire severity beyond which N-fixation inputs by Siberian alder are drastically reduced.

Fire reduces differences in alder growth traits (density, growth, and N-fixation) between deciduous- and black spruce-dominated stand types, but growth and N-fixation differences return by intermediate-age succession when the environmental factors that control growth and N-fixation (organic horizon depth, organic soil moisture, and likely soil temperature) begin to diverge among stand types. Yet, variation in alder density is independent of stand type, regardless of stand-age, and is controlled instead by soil moisture and fire severity. Sub-xeric/mesic to mesic sites of moderate fire severity contain the highest densities of alder. Under a scenario of higher fire severity, shorter fire return intervals, and larger fires, Siberian alder N-input is likely to increase in mesic to subxeric deciduous stands that burn at low to moderate severity. In contrast, sub-hygric to mesic stands of black spruce and/or stands that burn at moderate to high fire severity and return to black spruce will likely have the lowest Siberian alder density and N-input in the boreal forest. Black spruce stands that convert to and remain deciduous-dominant after high fire severity will likely have low densities of rapidly growing alders, but N-inputs are likely to increase over the long-term if alder in these stands continually propagate between successive low to moderate severity fires.

Classification maps showed a very dynamic pattern of changing Siberian alder N-input that varied across a burn severity gradient and across post-fire vegetation types. Siberian alder density and N-input generally increase across the landscape from pre- to post-fire, in areas that either remain or convert to a deciduous vegetation type. Gains from Siberian alder N-fixation are countered by N volatilization losses in areas that remained black spruce or mixed. High N volatilization in high fire severity black spruce stands is unlikely to be fully recovered by Siberian alder N-input (due to reductions in alder density); however, moderate-to-high fire severity black spruce stands are more likely to recover initial N-losses in the short-term because less N is volatized and more N is recovered compared to high fire severity black spruce stands. Interestingly, high Siberian alder N-inputs in deciduous stands may offset N-losses from pre-fire black spruce stands, which would result in a spatial redistribution of N pools.

Given the high Siberian alder N-input in moderately burned pre-fire black spruce and deciduous stands that follow a post-fire deciduous trajectory, combined with the higher rates of ANPP in deciduous versus black spruce stands, rates of post-fire C-sequestration are likely highest in post-fire deciduous stands that contain robust alder populations. Conversely, C sequestration rates would likely be very low in pre-fire black spruce stands that experienced high fire severity and converted to a deciduous trajectory because N-losses are highest and alder density, and therefore N-input, is lowest in this conversion pathway. Other ecological processes that are affected by Siberian alder distribution (e.g. aquatic productivity, soil acidification, and N nitrification) are also likely to show changes in spatial pattern and intensity across the landscape as a result of variable N-losses from fire and N-gains from Siberian alder N-input. The spatial distribution of alder clumps, or patches, within a stand-type was not covered in this study, but

will determine the heterogeneity of within-stand Siberian alder N-inputs and therefore the within-stand spatial pattern of N-recovery after fire.

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